EFFECTS OF GULF OF ALASKA SOCKEYE SALMON *(Oncorhynchus nerka)* ABUNDANCE ON SURVIVAL, BODY SIZE, GROWTH RATE AND AGE AT MATURITY OF BRITISH COLUMBIA AND BRISTOL BAY, ALASKA SOCKEYE POPULATIONS

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Effects of Gulf of Alaska sockeye salmon (*Oncorhynchus nerka*) abundance on survival, body size, growth rate and age at maturity of British Columbia and Bristol Bay, Alaska sockeye populations[1]

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ABSTRACT

Peterman, R.M. 1984. Effects of Gulf of Alaska sockeye salmon (Oncorhynchus nerka) abundance on survival, body size, growth rate and age at maturity of British Columbia and Bristol Bay, Alaska sockeye populations. Can. Tech. Rep. Fish. Aquat. Sci 1302:iv + 87 pp.

Data on marine survival and growth rates, adult body sizes and mean age at return are examined for six British Columbia and ten Bristol Bay, Alaska sockeye salmon stocks to determine if these variables reflect changes in the total abundance of sockeye salmon rearing in the Gulf of Alaska. Both B.C. and Bristol Bay sockeye stocks show significant effects of ocean abundance of similar-aged competitors, particularly on resulting adult body sizes at given ages. A series of tests identifies the late second or early third year of life as the most critical period for these effects, with adults of a given age returning 10 - 22% smaller when stocks encounter large numbers of competitors during this period. The distributions of sub-2 B.C. and Bristol Bay sockeye in the Gulf of Alaska overlap considerably during this period, thereby providing the opportunity for the types of indirect competitive interactions which could produce the relationships shown here. The rarity of significant effects of ocean abundance of salmon on survival or mean age at maturity in this study suggests that changes in predation or disease-induced mortality are probably not important effects of changes in abundance. But because of the effect of abundance on adult size and because of the cyclic pattern of total Gulf of Alaska sockeye abundance, it may be advisable to choose years for large releases from B.C. sockeye enhancement facilities so that those fish will be late age 2 or early age 3 during a low in the Gulf of Alaska sockeye abundance. This would maximize weight of adult returns per smolt released by avoiding times of severe competition with other fish in the Gulf. Lake fertilization is probably the most appropriate means to periodically produce large sockeye smolt abundances since it may be economically impractical to leave sockeye spawning channels unused in non-production years. Further studies are suggested concerning the biological interactions of stocks on the high seas and the evaluation of a proposed "pulsed production" strategy.

RÉSUMÉ

Peterman, R.M. 1984. Effects of Gulf of Alaska sockeye salmon (Oncorhynchus nerka) abundance on survival, body size, growth rate and age at maturity of British Columiba and Bristol Bay, Alaska sockeye populations. Can. Tech. Rep. Fish. Aquat. Sci. 1302:iv + 87 pp.

On examine les données sur la survie en mer, les taux de croissance, la taille adule et l'âge moyen à la remontée du saumon rouge appartenant à six stocks de la Colombie-Britannique et à dix stocks de la baie Bristol (Alaska) afin de déterminer si ces variables traduisent les variations du nombre total d'individus utilisant le golfe d'Alaska comme aire de croissance. L'étude de ces stocks montre les effets importants de l'abondance océanique de compétiteurs du même âge surtout pour ce qui est de la taille adulte à un âge donné. Une série d'expériences a révélé que la fin de la deuxième ou le début de la troisième année du cycle vital est la période la plus critique; ainsi, lés adultes d'un âge donné retournant aux frayères natales sont de 10 à 22 % plus petits quand les stocks rencontrent un grand nombre de compétiteurs pendant cette période. La répartition de saumons rouges de moins de 2 ans provenant de la C.-B. et de la baie Bristol se chevauche considérablement dans le golfe d'Alaska à ce moment, ce qui favorise donc le genre de compétition indirecte qui pourrait engendrer les relations étudiées dans le présent document. Le peu d'incidence de l'abondance océanique du saumon sur la survie ou sur l'âge moyen à maturité porte à croire que les variations de la prédation ou de la mortalité due à la maladie n'ont probablement pas d'effets importants pour l'abondance. Cependant, à cause de l'incidence de l'abondance sur la taille adulte et de la variation cyclique du nombre total de saumons rouges dans le golfe d'Alaska, il conviendrait peut-être de choisir des années pour le lâcher massif à partir d'installations d'élevage du saumon rouge en C.-B.; ainsi, ces poissons auraient atteint la fin de la deuxième ou le début de la troisième année quand le nombre de saumons rouges dans le golfe d'Alaska serait faible. En soustrayant le poisson à la compétition intense avec d'autres individus présents dans le golfe, on porterait au maximum le poids de l'adulte remontant par rapport au saumoneau relâche. La fertilisation de lacs est probablement le meilleur moyen de produire périodiquement un grand nombre de saumoneaux rouges car il pourrait etre économiquement irrealisable de laisser les frayères artificielles de cette espèce inutilisées pendant les années non productives. On propose de plus amples études sur les interactions biologiques entre les stocks en haute mer et l'évaluation de la stratégie proposée de "production modulée".

INTRODUCTION

In Pacific salmon (Oncorhynchus spp.) fisheries research there has been relatively little empirical work done on density-dependent effects of stock abundance in the ocean. The papers by Davidson and Vaughan (1941), Mathews (1980), Peterman (1978), Ricker (1982) and Rogers (1980) examine the effects of marine abundance on body size and survival rate and do in some cases report significant effects. However, none of those cases deals with total abundances in the ocean; most only examine within-stock abundances, catches as an index of abundance, or abundance at time of maturity instead of at some earlier time when size and survival could also potentially be affected by abundance.

The approach I take here is to relate reconstructed total abundances of sockeye salmon (O. nerka) residing in the Gulf of Alaska to marine survival rates, adult body sizes by age, marine growth rates and mean age at return for each of several stocks. These reconstructed minimum ocean abundances are derived from historical records of abundances of catches and escapements by age for all British Columbia and Bristol Bay, Alaska sockeye stocks (see Peterman and Wong 1984 for details). Those stocks comprise the majority of the sockeye which reside in the Gulf of Alaska. The reconstructed ocean abundances show three important features: 1) an inverse relation in abundance of British Columbia and Bristol Bay stocks of ages greater than 2; 2) significant lags in the abundance cycles of sockeye from those two regions; and 3) a failure of these abundance cycles to drift into synchrony during the years examined, as would be expected from the different ages of maturity of fish in these two regions (Peterman and Wong 1984). One possible explanation for these observations is some form of interaction among sockeye stocks in the Gulf of Alaska. If the dynamics of sockeye salmon stocks are affected in a major way by the abundance of conspecifics in salt water, then this influence should be reflected by changes in marine growth rates, size and age distributions, and/or survival rates as total sockeye abundance varies in the Gulf of Alaska. The present study of the relation between these types of variables and total sockeye abundance was stimulated by the above observations on the time series of abundances as well as by the need for a broader view of fish stock dynamics as stated by Rigler (1982).

Since previous work has shown that there are density-dependent effects within stocks on size and survival (e.g. Rogers 1973; Peterman 1982a), the present analysis tests if the influence of total Gulf of Alaska sockeye abundance is significant even when within-stock abundances are taken into account. This is done by using multiple regression as detailed below, where within-stock abundance is one independent variate and total Gulf of Alaska sockeye abundance ' the other.

This work is intended to be exploratory only in that it analyzes evidence relevant to hypothesized interactions among sockeye on the high seas without attempting to empirically identify the details of specific mechanisms leading to those interactions. If interactions are identified then such follow-up work on those specific processes would be in order. Several types of interaction can be hypothesized. 1) Competition for food: large abundances of sockeye in the Gulf of Alaska could temporarily decrease the food supply which could result in slower growth rates, smaller adult body sizes and possibly lower-than-expected survival rates. 2) Predator aggregation: large abundances of sockeye could cause aggregation of predators. If these predators (such as seals) select prey from the large end of the size distribution, this could lead to the same observed effects as competition, noted above. If predators selectively remove the small end of the size distribution, survival rates would be lower but larger-than-average adults would result. 3) Incidence of disease: if diseases spread more quickly in large populations, then their effects will be the same as the predators, depending on their host size vulnerability. If vulnerability does not vary with size, then no net effect other than decrease in survival would be seen. 4) Combination of hypotheses 1) and 2) above: for predators that selectively remove larger prey, the effects of competition will be exacerbated. If predators remove small prey instead, then the decrease in size due to competition might be cancelled out, leaving fish of about normal size but fewer of them, i.e. there would be no apparent change in size but survival rate would be lower than expected. 5) Combination of hypotheses 1) and 3): similar effects as 4).

METHODS

DATA BASE

In the Gilbert-Rich notation age 4_2 indicates that a sockeye salmon is in its 4th total year of life, and that it entered the ocean during its second year (hence called a sub-2 fish), after rearing one winter as a fry in freshwater. Total age is increased each spring when the fish enter the next year of life. All of the British Columbia sockeye stocks used (or subpopulations of them) in this analysis are sub-2 fish but the Bristol Bay stocks have large numbers of both sub-2 and sub-3 fish. Most sockeye salmon reside in the ocean between 2.25 and 3.25 years; ages 4_2 and 5_3 exemplify the former and ages 5_2 and 6_3 the latter. Only small numbers of sockeye reside in salt water for periods outside that range.

Independent Variates

There are two main types of data used in this analysis. Measures of sockeye abundance in the Gulf of Alaska comprise the independent variates and measures of size, growth, survival and age at maturity, by stock, make up the dependent variates. Included as independent variates are within-stock ocean sockeye abundances and total Gulf of Alaska sockeye abundances. Both the within-stock and total Gulf of Alaska sockeye abundances were estimated in a similar way, by applying Fry's (1949) virtual population analysis to the annual number of fish in catches and escapements, by age. Details on the methods and assumptions behind these reconstructed ocean sockeye abundances are given in Peterman and Wong (1984). Briefly, catches and escapements by age to each statistical area in British Columbia and each stock and district in Bristol Bay were used to estimate minimum ocean sockeye abundances, by age, from the early 1950s to mid-1970s. The Alaskan data include estimated Japanese high seas catches (see Peterman and Wong 1984). Virtual population analysis estimated the abundance of age 4 sockeye in the ocean in 1974, for example, by summing up all the known returns (=catches and escapements) for the given cohort (age 4 returns in 1974, age 5 returns in 1975, age 6 returns in 1976, etc.). This procedure was done for all statistical areas in B.C. and Bristol Bay to get the minimum total Gulf of Alaska sockeye abundance, by age, and by ocean residence year (ORY). There were no significant linear time trends in these reconstructed ocean sockeye abundances. Sources of the total

B.C. and Bristol Bay data are noted in Peterman and Wong (1984). In the above example, the abundance figure for age 4 sockeye (say 30 million) for ORY 1974 would be the minimum estimate of age 4 fish present in the Gulf from fall 1973 to fall 1974. It is a minimum estimate because stock- and year-dependent survival rates between ages are unknown for most stocks and so abundances could not be inflated as each cohort was followed backwards through ages, as in Gulland's (1965) virtual population analysis. The same procedure was applied to catch and escapement data for several individual stocks to obtain within-stock abundances. These data were mainly from unpublished records of the Alaska Department of Fish and Game (ADFG), Canada Department of Fisheries and Oceans (DFO), and International Pacific Salmon Fisheries Commission (IPSFC), (Appendix A, Table A1).

The minimum ocean sockeye abundances noted above represent estimates of abundances from the fall of one year to the fall of the next year because the late summer-fall period is when catches and escapements are enumerated. There are no estimates available for intervening periods. To simplify terminology, I define the age category of a given abundance during a given fall-to-fall period as the age reached at the end of that period, recognizing that the total fish age was incremented by one during the intervening spring. For example, what I call ocean abundance of age 4_2 fish in ocean residence year 1974 actually represents the abundance of the cohort which was age 3_2 from fall 1973 to spring 1974 and age 4_2 from spring 1974 to fall 1974.

Dependent Variates

Sixteen different stocks with a total of 26 different sub-populations are analyzed (sub-2 and sub-3 smolts being called different sub-populations). Data on the dependent variates come in several forms, depending on what types of samples were taken historically for each stock (Appendix A, Table A2). Detailed explanation is necessary for these dependent variates. All four Fraser River sockeye stocks considered here (Table A1) have mean standard body length data for age 4_2 fish on the spawning grounds, by sex. For two of those stocks (Adams and Chilko), average weights of 4_2 fish caught by United States purse seines are also available but are reliable only for their respective dominant cycle years because of overlap in run timings with other stocks. As noted in Table A2, some stocks only have sizes of maturing fish measured from

samples of the escapement, weighted by sex, whereas other stocks have more complete information from escapement samples plus commercial catch samples. In the latter cases an overall weighted mean body size of recruits by age is calculated by Yuen et al. (1981). In each case, I used the most complete information available. For those few stocks where extensive smolt abundance data exist, marine survival rates can also be calculated. The first form of survival rate data is $\log_e$(adult abundance/smolt abundance); the log transformation is made to normalize the distribution based on findings of Peterman (1981). The second form is a residual in marine survival rates, or deviation from what is expected by the best-fit smolt-to-adult relation. This residual for each brood year i (v_i) is

$$v_i = \log_e \left(A_i/(cS_i^k) \right)$$

where A_i is the total adult returns for brood year i, S_i is the smolt abundance for that brood year, and c and k are constants specific to each stock (Peterman 1981). For Babine Lake sockeye, the c and k parameters used are from the best fit regression corrected for smolt enumeration errors (Peterman 1982a). For the Chilko, Naknek and Ugashik stocks the geometric mean functional regression parameter estimates (Ricker 1973) are used because no data exist for smolt estimation errors. Long-term smolt abundance estimates are not available for other stocks.

There are several other dependent variates for the Babine Lake sockeye. Adult body size by age is available in two forms, from commercial gillnet samples (Jenkinson and Bilton 1973 and prior publications in that series; see Peterman and Wong 1984 for full list) and from test fishery samples (Kadowaki 1981). Both sources of size data are used in separate analyses because commerical fishery samples cover only 1952-1972 and test fishery samples from 1966-present. Adult body sizes of Babine Lake sockeye estimated from test fishery samples are more closely correlated with body sizes of the pre-recruit population than commercial gillnet samples because of gear selectivity (see Appendix B). But sizes from commercial gillnet samples are still useful indices of size for years in which test fishery data are not available.

Adult sockeye salmon body size generally reflects marine growing conditions more than freshwater conditions because most growth occurs in salt water. Smolt sizes of stocks examined here typically range from approximately 8-12 cm (4-15 g) and adults from 50-65 cm (1500-3500 g). Killick and Clemens (1963, p. 56), for example, document that 99% of the growth in weight of Fraser sockeye occurs in the marine environment. This is less true of fish lengths, which comprise most of my size data, so I calculate growth rates from smolts to the specified age in the four stocks in which smolt length data are available. I use the instantaneous growth rate computed from lengths, $\log_e$(size at age i/smolt size) (Ricker 1975 p. 207). Given the lack of scale measurement data in each of the stock-age-year combinations, it was not possible to do a more accurate back-calculation of growth rates, which would be desirable due to possible size-selective mortality (Ricker 1969). While instantaneous growth rates are usually applied to studies of growth over short periods, the growth rates over 1+ to 3+ years are still useful indices for comparisons across brood years but within stocks (Ricker 1979, p. 685).

Mean age at maturity is calculated for each brood year's offspring by taking the mean age of total brood year returns, weighted by the relative abundance of returns at each age. Table A2 lists the dependent variables analyzed for each sub-population, and Table A3 gives literature sources and detailed descriptions of those variates arranged by variate number for easy cross-reference.

STATISTICAL ANALYSIS

The main question addressed here is whether the total Gulf of Alaska sockeye abundance (X_2) significantly affects dependent variates such as growth, survival and age at maturity when the within-stock abundance (X_1) is also taken into account. A multiple linear regression model is fitted:

$$Y = a + b_1X_1 + b_2X_2 \qquad (1)$$

where,

Y = dependent variate such as marine survival rate, growth rate, or mean age at return for the cohort. These variates are transformed where necessary to make them normally distributed, as described above.

X_1 = within-stock abundance of age group in question.

X_2 = total Gulf of Alaska sockeye abundance of age group in question.

a = Y intercept in regression equation.

b_1 = regression coefficient associated with X_1.

b_2 = regression coefficient associated with X_2.

I test the null hypothesis (H_o) that $b_2=0$ by the standard method (Ott 1977 p. 472) using an F ratio to determine if the addition of X_2 to a regression on X_1 significantly decreases the residual sum of squares. The significance level for rejection of H_o is 0.05. For comparisons of b_2 values across stocks and ages, the multiple regression is also fitted after the X and Y variates are converted into standard deviation units (SDU).

Blocking of Data by Lag

The most common view among salmon biologists is that the early ocean residence is most critical for survival and growth (Parker 1968; Ricker 1976). However, Rogers (1980) found that adult body sizes of spawners were inversely correlated with total abundance of Bristol Bay fish that returned as adults during those same years. It is therefore not clear *a priori* whether interactions among sockeye in salt water will be most intense during early, middle or late ocean residence. Thus, all analyses are performed here for different assumed critical periods of interaction, ranging from the ocean entry year (OEY) for smolts to as late as 3 years after ocean entry (OEY+3). These different blockings of data are symbolized as ocean residence year (ORY)=OEY, OEY+1, OEY+2, or OEY+3. As an example, assume that the total Gulf of Alaska abundance of age 3 sockeye is as follows:

Ocean residence year	X_2 Abundance (Millions)
1966	21
1967	17
1968	60
1969	26

To determine, for instance, the period of ocean life in which the high seas abundance of age age 3 fish most affects the body size of maturing 5_2 Babine Lake sockeye, four different multiple regressions are done with equation (1). For the test of the hypothesis that the abundances in the year of ocean entry have significant effects, the time series of age 5_2 Babine stock body sizes is lined up so that the size of 5_2 fish which were spawned in 1964 (and which entered the ocean in 1966) is paired with the value of 21 million for X_2 (the number of age 3s present during ocean residence year 1966). This is for the so-called ocean entry year (OEY) analysis; for OEY+1, 17 million would be paired with that same brood year 1964 body size of age 5_2 fish, and so on for the other ocean residence periods. These different ocean residence periods are also referred to in this paper as lags, since they cover different periods after fish enter salt water. These various lags, OEY, OEY+1, OEY+2, and OEY+3 have specific interpretations here; they correspond to the approximate ocean residence periods of the first 4 months, months 5-16, months 17-28, and months 29-40, respectively. These particular periods result from the relative timing of smolt entry into salt water, of adult enumeration, and of estimation of high seas abundances. Most sockeye stocks analyzed here have late spring smolt migrations and early fall spawning. Thus, there are approximately 4 months between the time of smolt migration and the time when estimates of ocean sockeye abundances are updated in the fall (see Fig. 1). Thus, the first ocean residence period is only 4 months long; new abundance estimates then apply during each subsequent 12-month period. For simplicity of discussion I use this average of 4 months, recognizing that at one extreme this period is 2 months for most Bristol Bay sockeye and at the other extreme 6 or more months for some B.C. stocks. These small differences do not affect the interpretations here because I examine several alternative lag hypotheses which differ by 12 months. Note that the OEY+3 analysis is run only for those fish which are in the ocean one year longer than age 4_2s (5_2 or 6_3 fish). Similarly, analyses with lag OEY+2 are not run for the age 3_2 or 4_3 Y variates

because these fish have already matured by that time and are no longer resident in the ocean.

Blocking of Data by Age

It is also not clear a priori which age group abundances of sockeye may be the most important ones influencing the dependent variates such as size, survival and age at maturity. Therefore multiple regressions are done by using different age categories of abundances in separate analyses. Abundances of each of ages 2 through 6 are used separately and 4 summed categories are used: age 2+age 3, age 4+age 5, all ages >2, and all ages. These age groupings implicitly permit examination of effects of several types of processes by combining ages which are most similar in size and which presumably have similar effects on food supplies or predators. In a given multiple regression I use the same age category for the within-stock abundance (X_1) as the total Gulf of Alaska sockeye abundance (X_2). I do not mix age categories in the analysis by using, for example, age 3 abundances for X_1 and age 4 abundances for X_2. Such mixed cases are not as consistent with biologically plausible mechanisms as cases which use the same age category.

Number of Significant Cases

In exploratory studies such as this one, where large numbers of hypothesis tests are being made with many sets of data, it is necessary to recognize that roughly 1 out of 20 tests are expected to be significant at the $\alpha=0.05$ level by chance alone. Therefore, I show for each group of tests the probability of getting the observed number of rejections of the null hypothesis by chance alone. Knowledge of those probabilities will reduce the likelihood of being misled by chance relations. Those probabilities are determined in three different ways depending on sample size, n. If $n \leq 50$, probabilities are read directly from tables of the binomial distribution for individual terms (National Bureau of Standards 1952). The Poisson approximation to the binomial is used when $50 < n < 100$ and $\alpha=0.05$ (Parsons 1974). For larger samples, the normal approximation to the binomial is used since the following conditions are met here: $\alpha=0.05$, $n \geq 100$, $n\alpha \geq 5$, and $n(1-\alpha) \geq 5$ (Parsons 1974).

Correlations between X_1 and X_2

Correlation coefficients are calculated between the ocean abundance of an age group of a single sockeye stock (X_1) and the total Gulf of Alaska sockeye abundance of that age group (X_2). Those data are then used indirectly in the interpretation of multiple regression results since the X_1 and X_2 used in these regressions are not completely independent due to the inclusion of X_1 in X_2. To reduce this problem of multicollinearity between the two independent variables, it intuitively seems that the regressions could be formulated in terms of the abundance of a single stock (X_1) and the abundance of other stocks (X_2-X_1). However, this would not eliminate multicollinearity because synchronous cyclic dominance exists among several stocks. More important though, it turns out that such a procedure would be exactly equivalent to what is already done:

Define for any age group and stock the abundance in the ocean of that age of other stocks as $X_3 = X_2 - X_1$. X_3 will therefore be different for each stock. In this situation the multiple regression equation would be:

$$Y = a + b_1X_1 + b_3X_3 \qquad (2)$$

However, in terms of the sum of squares errors (SSE), probabilities, and testing of H_o:$b_3 = 0$, this is equivalent to the multiple regression analysis for X_1 and X_2 as indicated below.

Given $X_3 = X_2 - X_1$,

then $X_2 = X_3 + X_1$

From model (1) above we have

$$Y = a + b_1X_1 + b_2X_2 \qquad (1)$$

substituting for X_2 into eqtn.(1)

$$Y = a + b_1X_1 + b_2(X_3 + X_1)$$

$$= a + b_1X_1 + b_2X_3 + b_2X_1$$

$$= a + (b_1 + b_2)X_1 + b_2X_3 \qquad (3)$$

In both eqtn. (2) and (3), we end up with a regression on X_1 and X_3. The slope on X_3 is b_2 in eqtn. (3) and b_3 in eqtn. (2). Therefore b_2 and b_3 will come out identical, as will their probabilities for the tests for slopes = 0. Hence, from the standpoint of my analyses of the importance of ocean sockeye abundance, results will be identical whether eqtn. (1) or (2) is used. Furthermore, the biological interpretation of the slope of $X_1(=b_1 + b_2)$ in eqtn. (3) is not meaningful. Therefore I use the multiple regression on X_1 and X_2 as indicated by model eqtn. (1).

Equation (1) implies that there is an effect on a dependent variate attributable to, a) within-stock influences (X_1) which at a minimum would occur early in the fish's life or very late as the fish return to home streams, and b) influences of all sockeye present (X_2) regardless of origin. However, because of the identical outcome of the two different approaches noted above, it is not possible to distinguish whether X_2 (all sockeye) or X_3 (other sockeye) is the most influential ocean sockeye abundance on the dependent variates.

IMPRECISE ESTIMATES

Because many of the independent variables used in this study are estimated imprecisely, the regression results are subject to the usual problems of interpretation, namely, the estimated slopes are lower in absolute value than the true slopes (Ricker 1973). For example, the estimates of ocean abundances of sockeye include some cases where escapements are crudely estimated and this imprecision is therefore likely to cause fewer rejections of the null hypothesis that $b_2=0$ than if true abundances were known. Therefore, the number of significant density-dependent cases discussed here is a conservative estimate.

RESULTS

GENERAL

Correlations between X_1 and X_2

Table 1 shows the correlations between ocean abundances of a given sockeye stock and age (X_1), and total Gulf of Alaska sockeye abundance of that age (X_2). Note that many Bristol Bay stocks show large positive correlations for two reasons: 1) cyclic dominance and the coincidence of peak abundances among some of those stocks keep them in synchrony, and 2) Bristol Bay stocks are very abundant relative to B.C. stocks and therefore the larger populations such as Kvichak comprise a significant portion of the total Gulf of Alaska abundance. These characteristics pose problems for interpretation of the multiple regression results because in cases where the X_1-X_2 correlation is high, X_1 is not independent of X_2; significant results for the effect of X_2 may be partially due to the significant effect of X_1, and vice versa. This difficulty was recognized from the beginning but there is no practical solution. B.C. stocks show smaller correlations between X_1 and X_2 and therefore pose fewer problems of interpretation of regression results.

Critical Ages and Lags

Because I am mainly interested in the importance of the total Gulf of Alaska sockeye abundance, Tables 2-4 summarize the results for the tests of the null hypothesis (H_0:b_2=0) that the total sockeye abundance in the Gulf of Alaska (X_2) does not significantly affect dependent variables. Recall that this null hypothesis is tested for multiple regression results in which any within-stock abundance (X_1) effects are taken into account. Table 2 covers British Columbia stocks only and shows by age and by ocean residence period the proportion of regression tests in which H_0 is rejected, i.e. in which X_2 has a significant effect. For example, the second row under the age 2 column in Table 2 shows that 29 different multiple regressions of Y variates on X_1 and X_2 were performed, using age 2 abundances for X_1 and X_2. The 29 dependent variates used in these different regressions are the ones listed under British Columbia stocks in Table A2. The first four rows of Table 2 under the heading

"ORY=OEY" reflect the analyses which use the abundances in the ocean residence year equal to the ocean entry year. As defined previously then, this example uses the within-stock and Gulf of Alaska sockeye abundances of age 2 fish estimated at the end of the first four months after the fish entered salt water. Three of the 29 regressions reject H_0, and the probability of getting 3 rejections out of 29 tests at $\alpha=0.05$ is shown in the fourth row as 0.12 (National Bureau of Standards 1952). Tables 3 and 4 show similar statistics for the sub-2 and sub-3 Bristol Bay stocks.

A simple method is used to identify the most important period for effects of ocean sockeye abundance. First note the right-hand "sum" column in Tables 2-4. Several lags show a significant probability for obtaining the indicated sum of number of rejections of $H_0:b_2=0$. For British Columbia stocks, the highest proportion (9.5%) of significant effects of total Gulf of Alaska sockeye abundance arises during the second lag (ORY=OEY+1). The probability of obtaining the stated number of rejections of the null hypothesis is < 0.001 (Table 2). Bristol Bay sub-2 fish show results similar to those for B.C. stocks; the highest proportion of significant b_2 values, 7.1%, also occurs in the ORY=OEY+1 tests (Table 3) and with P=0.015. In contrast, the sub-3 Bristol Bay fish show the highest proportion of significant cases, 7.4%, in the ORY=OEY analyses, with P=0.014 (Table 4).

Thus, the most critical period for the effect of ocean sockeye abundance is the period approximately 5-16 months after ocean entry for British Columbia stocks (all sub-2s here) and for sub-2 Bristol Bay stocks, but roughly the first 4 months for sub-3 Bristol Bay fish. As noted earlier, abundances are estimated for the end of each of these periods when, in both smolt types, fish are in their third year of life (Fig. 1). Therefore, it is possible that for British Columbia sub-2 stocks and for both Bristol Bay smolt types, the fish are age 3 when the most frequent significant interactions with ocean sockeye abundance are seen. In the case of sub-2 stocks, fish are also late age 2 during the critical OEY+1 period (Fig. 1) so the importance of age 3 above is not certain. This critical late age 2 to early age 3 will be termed the target age. Note that in all of the cases cited, the high percentage of significant b_2 cases is higher than would be expected by chance alone, as shown by the corresponding probability values in Tables 2-4.

It is clearly recognized that the interpretation of these probability results is largely qualitative because not all the hypothesis tests are independent. Some of the Y variates are related (e.g. mean length and growth rates) and some of the age categories are not independent, such as "age 2" and "age 2+3". This lack of independence means that the probabilities shown in Tables 2-4 are too low. But since this bias affects all lags (OEY, OEY+1, OEY+2 and OEY+3), it is unlikely that the choice of critical lag would be affected. As a check, I summed the results for significant cases only using the non-combined age columns in Tables 2-4 (age 2, age 3, ...age 6), which are independent cases. Exactly the same conclusions were reached and differences between lag categories became more pronounced: the highest proportions of significant cases still occur with lags OEY+1 for B.C. and Bristol Bay sub-2s and with OEY for Bristol Bay sub-3s. Similarly, in deciding on the most important age categories of X_1 and X_2 abundances, I might make an incorrect decision because of lack of independence among some dependent variates. But the relative importance rankings among ages will remain unchanged even if the bias is somehow removed because related Y variates are tested in all age categories. As will be shown, the consistency of the results across stock groups which show late age 2 to early age 3 to be the critical target age strongly suggests a real underlying pattern, regardless of the difficulty of unambiguously establishing that pattern.

Tables 2-4 also indicate which age categories of Gulf of Alaska sockeye abundances are the most important influence on the late age 2 to early age 3 fish identified above. These ages, called the influential ages here, are found by examining the probabilities of obtaining the observed number of significant results in each of the age categories within the most important lags (OEY+1 for sub-2 fish, OEY for sub-3s). For B.C. stocks, age categories 5 and 2+3 show the most cases where the effect of X_2 is significant when ORY=OEY+1 and where the probability of obtaining the given number of significant cases is less than 0.05 (Table 2). In the ages 2+3 category, the one with the largest number of rejections of H_o:b_2=0, 31% of the tests show a significant influence of ocean sockeye abundance of ages 2+3 on the dependent variates. This strongly suggests some important influence of similar-sized fish on the late age 2- early age 3s of the target stocks. The importance of

the age 5 category also suggests an influence of older fish on these late age 2 to age 3 fish. For sub-2 Bristol Bay stocks with ORY=OEY+1, the influential ages are ages 3 and "all ages combined" (11.9% and 14.3% of the cases significant, respectively) (Table 3). Sub-3 Bristol Bay stock results in Table 4 show the abundance in age categories 4+5 and > 2 are the most influential in the most important lag, ORY=OEY.

SPECIFIC CHANGES IN DEPENDENT VARIATES

Below is a description of the details of the multiple regression results. The discussion focuses on the cases of significant relations between X_2 and the dependent variates which appear in the most important lags and age groupings, as defined in the preceding section. This procedure reduces the likelihood of focusing on spurious relations. As well, cases within lags and age groupings can be examined to determine whether results are consistent or whether there is simply a large number of significant, but contradictory results. To summarize, the important lags and influential age abundance categories are as follows: B.C. stocks--lag ORY=OEY+1, ages 2+3 and 5; Bristol Bay sub-2 stocks -- lag ORY=OEY+1, age 3 and "all ages"; Bristol Bay sub-3 stocks--lag ORY=OEY, ages 4+5 and >2.

Table 5 lists regression results for all those cases in which $H_0: b_2=0$ is rejected in the important age categories and lags, as defined above. Only a few representative examples of the results in Table 5 are illustrated here by plots, so the discussion below refers to regression results by case number (first column in Table 5) as well as by Figure number (last column).

Body Size and Abundance of Younger Ages

The b_2 slopes for cases 1-9 and Figs. 2-6 illustrate for British Columbia sockeye stocks the consistent negative effect of age 2+3 abundance of all sockeye stocks in the ocean during lag OEY+1 on adult body size and growth rate. For example, the regression equation $Y=54.83 - 0.459X_1 - 0.035X_2$ plotted in Fig. 2 shows that age 4_2 females of the Chilko Lake sockeye stock are smaller for brood years in which those females are in the ocean as late age 2- early age 3s at the same time as large numbers of ages 2 and 3 sockeye of all B.C. and Bristol Bay stocks. In other words, those females reflect density-dependent growth. Chilko L. males show almost identical effects of X_2

abundance on age 4_2 size (Case 2, Table 5). Similar effects of ages 2+3 abundance are shown by Stellako (both male and female), Owikeno and Babine sockeye stocks (Cases 4-7, Figs. 3-5). In neither Fig. 4 nor 5 is the illustrated positive slope on X_1 significant (Table 5). Instantaneous growth rates to age 5_2 for Babine fish, which take into account variable smolt size as well as adult size, also decrease with greater age 2+3 sockeye abundance in the ocean (Fig. 6). While the slope of growth data from the test fishery on X_2 in Case 9 is largely determined by one data point at X_2=78 x 10^6, the slope in standard deviation units is within 8% of the slope in Case 8 shown in Fig. 6, which reflects 4 additional years of data and which derives all its points from commercial gillnet samples. Mean weight of age 4_2 Chilko sockeye caught by U.S. purse seines in their cyclic dominant years also shows a significant decrease in size with increasing X_2 abundance (Case 3), although with only 4 data points this result is not important on its own; it merely corroborates the other findings. In cases 1-9 for the B.C. stocks, note that between 30 and 85% of the variability in the dependent variates is accounted for by the multiple regression fit, as shown by the multiple r^2 values (Table 5). To summarize for B.C. sockeye, there is a consistent negative effect of X_2 abundance in the ages 2+3 category on size and growth. Since the age at which most effects of X_2 occur is late age 2 to early age 3, this result may be due to the similar size of age 2 and 3 fish, which may be influenced by the same food or predator species.

Some Bristol Bay sub-2 sockeye also show the same negative effects of abundance of young conspecifics as B.C. stocks (Figs. 7-8), using the appropriate lags of OEY+1. Multiple r^2 values range from 41 to 48% in these Figures. The positive slope for the effect of the within-stock abundance in Figure 8 is not statistically significant. There are only two exceptions to the trends shown in the age 3 and 2+3 abundance categories in the first 13 cases for B.C. and Bristol Bay stocks. The first is the significant positive slope of age 3_2 length on X_2 abundance for Wood River sockeye (Case 12). But this result may be heavily influenced by the single extreme point at high X_2 abundance. The other exception is the positive effect of X_2 on Togiak age 4_2 lengths (Case 13), for which there are two outlier points at high X_2 abundance.

Fig. 8 is an example of a stock, the Egegik River stock, where within-stock (X_1) abundances are highly correlated with ocean sockeye abundances (X_2) of the same age. For the age 3 category shown in this plot, r=0.92 between X_1 and X_2 (Table 1) because the cyclic dominance pattern of this low abundance stock coincides with that of the much more abundant Kvichak R. stock. Thus, even though H_0 of b_2=0 is rejected in this plot, one is much less able to attribute a unique effect to the total ocean abundance than in cases where the correlations between X_1 and X_2 are lower.

Body Size and Abundance of Older Ages

For B.C. stocks with the OEY+1 lag, three stocks show a significant influence of age 5 fish, the only older age category important for B.C. sockeye. Cultus and Stellako sockeye show a positive effect of age 5 X_2 abundance on standard lengths of age 4_2 fish in the escapement (males only for Cultus, both sexes for Stellako), and Adams River sockeye show the same effect on weight of 4_2s but all four cases (14-17 in Table 5) are heavily influenced by a single extreme data point at large X_2 abundance. Thus, while these four cases show there may be a positive influence of age 5 fish on body size of B.C. fish, it is not convincingly established.

For Bristol Bay sub-2 sockeye with the OEY+1 lag, the total X_2 abundance of "all ages" has a consistent negative influence on adult body size and growth rate (Cases 18-22, Figs. 9-10). Note that the Kvichak stock is the most extreme case of high correlation between the within-stock abundance X_1 and X_2 abundances (Table 1) because it is by far the most abundant stock on the coast. This correlation tends to make the data points fall along a straight line in the multiple regression and the slopes of the fitted regression plane become very sensitive to a few data points that deviate from that line. The slopes and hypothesis tests for Kvichak sockeye are therefore more suspect than for other stocks. This may partly explain why this is the only stock shown in Cases 1-22 where the positive effect of X_1 is significant, a result opposite to the other examples where both X_1 and X_2 have negative effects or X_1 has no significant effect. However, the direction of the effects of total Gulf of Alaska sockeye abundance X_2, on Kvichak sockeye body size and growth rate are consistent with most other stocks.

For Bristol Bay sub-3 sockeye with the ORY=OEY lag (Cases 23-31), results are consistent within the important age categories except for the Naknek stock. Ugashik sockeye show a decrease in growth rates from smolts to age 5_3 and 6_3 as X_2 abundance of age 4+5 fish increases (Cases 23-24, Fig. 11). These results are consistent with those of other stocks presented earlier. Naknek sockeye, however, show an increasing body size for age 6_3 (Case 25) and increasing growth rate to age 5_3 (Case 26) with increasing numbers of age 4+5 fish. When the >2 age category is used for the X_1 and X_2 variates, the Naknek sub-3s again stand out because their significant trends are opposite to those of other stocks. The Nuyakuk, Ugashik and Egegik show a depressing influence of X_2 abundance on body size, (Cases 27-29, Fig. 12), whereas Naknek shows a positive effect on age 6_3 body size and growth rate (Cases 30-31). The oddity of the Naknek stock, to be discussed later, parallels the findings in a previous study (Peterman 1982b). In the category of effects of abundance of older ages on body size, results are much less consistent across stocks than in the previous section which dealt with abundance of young fish.

Mean Age at Return

Mean age at return data were only available for four stocks, Babine, Kvichak, Naknek and Ugashik, the latter three having data for both sub-2 and sub-3 populations. Only two cases in the previously-defined critical ages and lags show significant effects of X_2 abundance, Ugashik sub-2s a negative effect and Kvichak sub-3s a positive one (Cases 32-33). For the Kvichak case, the positive slope on X_2 is significant but the multicollinearity problem again precludes clear interpretation of this situation. Ugashik sub-2 fish have an earlier mean age at return as the abundance of age 3 sockeye in the Gulf of Alaska increases.

Marine Survival Rates and Their Residuals

Of the four stocks examined for this dependent variate, the Ugashik population is the only sub-2 stock which shows a significant effect of X_2 abundances in the critical age and lag categories (Case 34). In this case, as X_2 increases, survival rates are lower than expected from the smolt-to-adult relation. Ugashik sub-3 fish show a similar negative effect of the ages 4+5

abundance category on these residuals in marine survival (Case 35). There were 12 tests of density dependent marine survival or residuals in marine survival, and only the above two cases were significant, fewer than would be expected by chance alone ($P > 0.09$). In addition, the collection of signs of all these slopes on X_2 abundance, regardless of level of significance, does not show any significant tendency toward positive or negative values ($P > 0.5$).

DISCUSSION

CRITICAL AGES AND LAGS

Results presented here show that the abundance of conspecific populations in the Gulf of Alaska is an important variable which affects attributes of sockeye salmon stocks such as adult body size of given ages. The effect of high seas sockeye abundance is significant even when the effects of within-stock abundance are included. The findings in Tables 2-4 suggest that sockeye salmon are most frequently affected by abundance of Gulf of Alaska sockeye during their late second or early third year of life: British Columbia and Bristol Bay sub-2 fish exhibit the largest number of significant effects on dependent variates during their ocean residence year OEY+1, when they are late age 2 to early age 3 and Bristol Bay sub-3 fish show most effects with the lag ORY=OEY, when they are age 3. While no one else has looked at the particular set of variables covered here, these results corroborate the general results of other studies which show that early ocean life is a critical period for salmon. For example, Ricker (1976) shows that mortality is more severe in early ocean life than later and Peterman (1982a) identifies the first 15 months of ocean life (out of a normal maximum of 39 months) as most critical for Babine Lake sockeye marine survival. On a finer time resolution, my results here are also consistent with those of Ricker (1982) in that he shows a negligible effect on adult body size of the conditions encountered during the first ocean residence year. He defines this first ocean year as May-December of the ocean entry year, which is most similar to the lag OEY used here. The B.C. sub-2 stocks are the only ones common to our two studies and the results here also suggest that the first 4 months of ocean life are less important in determining adult size for those stocks than the next 12.

Based on our knowledge of the oceanic migrations of immature and maturing sockeye, extensive overlap of British Columbia and Bristol Bay sockeye stocks occurs in the Gulf of Alaska (Fig. 13). Specifically, data in French et al. (1976), French and Bakkala (1974), and Hartt (1980) show that by late winter or early spring of their first year at sea, significant numbers of Bristol Bay and northeastern Pacific sockeye (including B.C. fish) occupy the region between latitude 45° N to 55° N and longitude 150° W to 170° W. As the fish age, both B.C. and Bristol Bay fish continue to have considerable overlaps and it is only as the fish return toward spawning grounds that their overlap is eliminated.

The overlap of B.C. and Bristol Bay sockeye stocks in space and time thus provides the opportunity for the types of indirect interaction such as competition or effects on predators which are hypothesized in the first section of this paper. The sub-2 B.C. and sub-2 Bristol Bay fish are shown above to be mainly affected by ocean sockeye abundances when ocean residence year equals ocean entry year plus 1 (ORY=OEY+1), which corresponds to approximately months 5-16 after ocean entry. The distribution of B.C. and Bristol Bay fish during this period is covered by the last 8-month portion of Fig. 14A and all of Fig. 14B.

Since the 4-month-long OEY period is most critical for Bristol Bay sub-3 fish, only the first four months of the distribution given in Fig. 14A are applicable to these sub-3s. However, since these fish are still in the Bering Sea before September of their first year in the ocean (French and Bakkala 1974, Hartt 1980, Hartt and Dell, in press), the significant results found here for Bristol Bay sub-3 fish are probably largely attributable to interactions with other Bristol Bay sockeye stocks because few B.C. sockeye are ever found in the Bering Sea (French et al. 1976).

BODY SIZE AND GROWTH RATES

Seven sockeye stocks, four of them in British Columbia, show that the ocean abundance of age 3 or 2+3 sockeye adversely affects adult body size of given ages and growth rates to those ages. The only exceptions to these inverse relations are attributable to one or two extreme outlier points. By using historically observed ranges of abundance in the regression equations

illustrated in Figs. 2-5, body sizes can be shown to be reduced substantially when within-stock and total Gulf of Alaska sockeye abundances are high. As examples, Chilko Lake age 4_2 sockeye can have their body weight reduced by 22%, Stellako R. fish by 13%, Owikeno L. fish by 11%, and Babine L. fish by 10%. The negative effects of abundance on size at age is most consistent with the competition for food hypothesis mentioned in the introduction because the other hypotheses which could also lead to smaller sizes (size selective mortality by predators or parasites) should also decrease marine survival. Yet only the two sub-stocks of the Ugashik population show a change in marine survival with total ocean abundance of sockeye, and + and - signs for slopes of all survival relations tested do not differ significantly from equal frequency. While long series of marine survival data are definitely needed for many more sockeye stocks, current marine survival data do not show any trends. Food competition is also consistent with the fact that these inverse relations between size and abundance appear when we examine the effects on late age 2 or early age 3 fish by abundances of age 3 or ages 2+3 fish. The similarity of slopes of body size variates on Gulf of Alaska sockeye abundance of young ages is discussed in depth elsewhere (Peterman, 1984).

When abundances of older ages are used, there is generally the same inverse relation between adult body size and ocean abundance of sockeye but with more exceptions, even among those cases other than the B.C. ones which are suspect because of single outlier points. The Kvichak exceptions cannot be weighted heavily because of the serious multicollinearity problem and the only current possibility for the Naknek cases, which show positive effects of abundance on size, may be mechanisms discussed in Peterman (1982b). In that paper, I showed that the Naknek fish were the only ones examined that showed significant within-stock density-dependent survival and/or maturation rate. Perhaps Naknek fish suffer from increased size selective predation on small members of the population when both their abundance and total Gulf of Alaska abundances are high (Naknek is well correlated with X_2, see Table 1). This might give an apparent increase in adult body size and growth rates. There are two criticisms of this interpretation: 1) Naknek sub-3 fish show these effects but Naknek sub-2s do not, and 2) no decrease in marine survival rate is found in the Naknek sub-3 cases when X_2 is large. Thus there is no obvious explanation for the unusual Naknek stock results.

The effect of the abundance of older ages on future adult body size of young sockeye salmon suggests that size distributions of food for young fish may overlap considerably with those of older fish. There is, however, too little information on food particle sizes, by age for sockeye salmon to verify this interpretation. The most relevant data are LeBrasseur's (1966) in which he shows sockeye of 25-50 cm length have considerable similarity in the taxonomic composition of their food, except larger fish tend to eat more squid. No information is given, however, on the size distribution of food within each taxonomic group, for each size group of fish. Alternatively, the effect of abundance of older ages on younger fish may arise from the feeding of the larger fish on higher trophic status species. This may detrimentally affect productivity of lower trophic status species which are the main food for age 2 or age 3 salmon by shifting the species composition to less desired species. To my knowledge, no evidence exists to test this alternative for salmon.

The results for the effects of abundance of young Gulf of Alaska sockeye on body size and growth rate are more consistent across stocks than the effects of older-aged fish abundance. This consistency, along with the plausibility of the associated mechanisms and the conservative number of significant results mentioned previously, suggests that this study reveals real patterns, not spurious ones. Furthermore, density-dependent growth is documented for numerous marine fish species (see Ware 1980 for review) so it should come as no suprise to find it in sockeye salmon as well.

MEAN AGE AT RETURN

Despite the significant effects of ocean abundance of competitors on adult body size, only two stocks show significant effects on mean age at return. But those two cases show opposite effects and no logical interpretation can be made of the results. Since only four stocks have sufficient data available for this analysis, trends might appear if more stocks are examined.

MARINE SURVIVAL RATES AND THEIR RESIDUALS

Only one stock shows an effect of Gulf of Alaska sockeye abundance on marine survival rates. The Ugashik stock shows a decrease in survival residuals with increasing abundance, which may be a result of lower food consumption and the smaller size noted earlier. The general lack of significant effects on survival of other stocks, in combination with the numerous effects on body size suggest that interactions among sockeye salmon in the Gulf of Alaska are not generally severe enough to alter mortality. Marine survival data on many more stocks are needed to further test this conclusion.

INTERPRETATION OF BODY SIZE RESULTS

Several authors have documented that adult body sizes of widely separated sockeye salmon stocks are generally significantly and positively correlated so that large adults in one stock usually occur at the same time as large adults in other stocks (Godfrey 1958, Killick and Clemens 1963, Ricker 1982). Ricker (1982) also showed that "The major contribution to similarity in adult size of two groups of sockeye is made by length of ocean life." The similarities in body size fluctuations across sockeye stocks suggest that factors encountered by fish during their ocean residence are important determinants of adult body size. Those factors could be physical oceanographic variables such as temperature or biological variables such as food supply, abundance of size-selective predators, or abundance of conspecific competitors.

Only a few authors have examined the effects of biological oceanographic variables on salmon body size and because of lack of good time series data on food supply or predators, all of these studies focused on the effects of salmon abundance, as was done here. However, all but one of these studies used only catches as an index of abundance. Three papers dealing with pink salmon (Oncorhynchus gorbuscha) came to varying conclusions. Godfrey (1959) showed that odd-year British Columbia pink salmon generally have larger body sizes than even-year populations. Odd-year populations are generally more abundant as indexed by catch and this, in combination with the well-known two-year life cycle of pinks, suggests that genetic differences inherent in the even-and odd-year lines may be the major source of differences in body size

(Godfrey 1959). Davidson and Vaughan (1941) studied pink salmon populations in Clarence Strait in southeastern Alaska using an abundance index based on catches. They found that when abundance was high, individual fish were small (as indicated by large number of fish packed per standard case) and they hypothesized that this relation was due to competition for food in salt water. Semko (1939), cited by Fredin et al. (1977), showed an inverse relation between average body size of pink salmon and pink catches in western Kamchatka, U.S.S.R. Mathews' (1980) study of Puget Sound, Washington coho salmon (O. kisutch) came to a similar conclusion as the last two studies above. Mathews found that Puget Sound coho salmon are smaller in years in which their abundances in June (as crudely indexed by catches) are high. But he noted that size selective mortality and/or increased growth in the next few months makes up for this growth depression so that the final size of adult fish only three months later is not related to abundance, again as indexed by catch. Unlike these coho salmon, the sockeye covered in my study generally do not make up for lost growth in early ocean life when present with large numbers of conspecifics, even though they generally have a year longer than coho to do so. For sockeye, Killick and Clemens (1963) found no relation between Fraser River sockeye catches and variation in body sizes of age 4_2 fish from the averages for each four-year cycle. They felt the difference between body sizes among the four cycles (dominant, subdominant, and two off-year cycles) is mainly due to genetic differences. Ricker (1982) found that sockeye salmon body size is positively correlated with sockeye catches in the statistical area of concern but he acknowledges (p.11-12) that these results are probably an artifact caused by using weighted average body size of all catches in any year rather than size by age. Rogers (1980) used total run size (catch plus escapement) to estimate the effect of abundances on body size and he found for Bristol Bay sockeye salmon that adult body size, by age, decreases with abundance of the Bristol Bay sockeye run that year. He interpreted this to mean that density-dependent growth occurs in the last year of life, but he apparently did not examine other possible times of interaction. My OEY+2 lag would be the same as his return year for age 4_2 and 5_3 fish, and OEY+3 would apply to 5_2 and 6_3 fish and my ocean abundances include B.C. stocks whereas Rogers' did not. Since the tests performed here on all lags reveal that late age 2 or early age 3 fish are most severely

affected, and during the first 0-16 months in the ocean, this suggests that Rogers might have drawn a different conclusion if he had used ocean sockeye abundances estimated at times earlier than return year.

All of the above studies except that of Rogers (1980) used only catches to indicate the abundance of a given stock or a set of nearby stocks. But changing fishing effort, fishing gear and management regulations will cause these abundance indices to be biased by varying degrees so results from those studies should be interpreted carefully. Catches average about 40-60% of the total annual runs. In Rogers' analysis and my own, catch plus escapement data are used and hence abundance figures probably more accurately reflect true abundances. This is the case even though sockeye escapements, particularly in British Columbia, are in some stocks crudely estimated (Cousens et al. 1982). In both Rogers' paper and the current one, an inverse relation was found between body size and abundance.

One plausible explanation of these inverse relations is the effect of freshwater growth on adult body size. This hypothesis concerns stocks in which the cyclic dominance pattern of abundances coincides with peaks of X_2, total Gulf of Alaska sockeye abundance. In those cases, an inverse relation between sockeye fry size and abundance in freshwater (Foerster 1944, Burgner et al. 1969, Rogers 1973) would mean at least part of the smaller resulting adult body sizes could be due to effects in freshwater. Instantaneous growth rates from smolts to adults avoid the problem caused by this freshwater size effect by taking smolt size into account. These growth rate variates also show significant negative effects of ocean abundance similar to those found for adult body sizes (e.g. Cases 8, 9, 22-24). Therefore, this freshwater hypothesis appears relatively unimportant in my cases.

As mentioned previously, the observed inverse relations between ocean sockeye abundance and adult body sizes are most consistent with the hypothesis of food competition. There is an indication that predation, parasitism or the interaction of these two processes with competition are not important because few stocks show decreased brood class marine survival rates with increased abundance. Thus, whatever the effects of ocean sockeye abundance, they seem to be primarily reflected by changes in body size rather than survival. Indirect competition among sockeye salmon resident in the Gulf of Alaska could

occur through decreases in available food supply caused by large abundances of sockeye. This common effect of ocean sockeye abundance on all stocks resident in the Gulf of Alaska could explain the positive correlation in body sizes across stocks noted at the beginning of this section. Such indirect effects could also explain the inverse relation between ocean sockeye abundance and adult body size found here. Larger sockeye tend to eat more squid and fish than younger ones although all sizes of sockeye in the ocean feed on amphipods, copepods and euphausiids (LeBrasseur 1966, Manzer 1968). LeBrasseur also found that stomach contents were greatly affected by the type of oceanographic domain in which fish were sampled and hence by the type of food available. For example, immature and mature sockeye in the subarctic domain have few euphausiids in stomachs but have large amounts of euphausiids in coastal or Alaskan stream domains. Both LeBrasseur and Manzer found high percentages of empty stomachs (up to 28% in the former which were summer samples and 50% in the latter, winter samples).

Up to this point I have only discussed hypotheses dealing directly with biological variables which could explain the observed decrease in adult size with increased abundance of sockeye in the Gulf of Alaska present in months 5-16 of ocean life. Physical oceanographic hypotheses must also be addressed since it is well known that some fish are affected by changes in variables such as temperature and salinity (Cushing 1982). Killick and Clemens (1963) and Ricker (1982) showed that sockeye growth <u>increased</u> as surface water temperature at Ocean Station P (50^{o}N, 145^{o}W) <u>decreased</u>. As Ricker discussed, mechanisms behind this observation are not clear. This lack of explanation arises because both physiological fish growth processes and dynamics of the food species of salmon are likely affected differently by temperature. In a related study, the results of Mysak et al. (1982) do not make biological sense because the coherence between Fraser River sockeye weight deviations and ocean temperatures is highest at a lag of 3-3.5 years. Given the 4-year lifespan of most Fraser River sockeye this result relates adult weights (99% of which is put on in salt water as shown by Killick and Clemens 1963) to ocean temperatures which prevail while the fish are still in freshwater! Thus, the causal mechanism is not well-understood. While it is clear from Killick and Clemens (1963) and Ricker (1982) that higher ocean temperatures are correlated

with smaller adult sockeye, it is not clear how temperature effects could indirectly lead to the observed inverse relations between adult size and ocean sockeye abundance described in the current paper. For a temperature explanation to work, warmer temperatures which are correlated with smaller adults must also correlate with higher survival and hence larger abundance. These effects are unlikely because a) Killick and Clemens (1963) showed an inverse relation between temperature and marine growth and Henry (1961) reported a positive relation between marine growth and marine survival for Fraser R. sockeye, and b) conditions that are poor for growth are more likely to be poor for survival than good. In addition, the requirement of the temperature explanation that marine survival increase with abundance is not supported by the results in this paper.

OTHER STOCKS AND SPECIES

Other stocks of sockeye salmon besides B.C. and Bristol Bay fish mature in the Gulf of Alaska. However, these other populations are not included in the present analysis because they are either generally small in abundance relative to the two other major groups of sockeye stocks or long-term records of catch and escapement by age are not available. Other salmonids such as pink and chum salmon might also affect the same food supply (LeBrasseur 1966) or predators as sockeye so this work is simply a starting point. However, the next step of including data on abundances of these other species is difficult given the lack of their long-term population data. Other non-salmonid species may also indirectly interact with sockeye salmon although this group seems less important:

> Pacific salmon are by far the most abundant group of fishes inhabiting the epipelagic zone of the subarctic region of the North Pacific Ocean. Other than salmon only 37 species of fish have been reported in gillnet surveys in the epipelagic zone and these have been present in much smaller numbers and more limited range than salmon (Larkins, 1964, cited in Fredin et al. 1977). Only six species (albacore tuna, Atka mackerel, salmon shark, jack mackerel, Pacific herring and pomfret) could be classified as abundant and then only in some limited parts of the salmon's distribution (Fredin et al. 1977).

IMPLICATIONS FOR POPULATION DYNAMICS AND MANAGEMENT

When combined with results from other published works discussed above, results here have important implications for sockeye salmon management and for understanding sockeye population dynamics. It appears that sockeye marine survival rate is more affected by within-stock abundance (Peterman 1982a) than by Gulf of Alaska sockeye abundance, although survival data from many more stocks might change that conclusion. In contrast, body size at a given adult age appears to be affected not only by within-stock abundance, but also by abundance of nearby stocks (Davidson and Vaughan 1941; Rogers 1980) and all Gulf of Alaska sockeye (present analysis). The latter effect in particular could play a role in the maintenance of the asynchrony in abundance cycles between British Columbia and Bristol Bay sockeye abundances noted in Peterman and Wong (1984). Maturing females which are 10 - 22% smaller than normal because of high abundances encountered in the Gulf will have significantly lower fecundity, which will in turn affect subsequent stock dynamics.

The potential for interactions among separate sockeye salmon stocks in the Gulf of Alaska suggests that we need broader means of evaluating the potential for success of various management manipulations. For example, attempts to increase abundance of sockeye salmon through enhancement may adversely affect other stocks through decreases in body size, and by focusing benefit/cost analyses only on the enhanced stock, the benefits might be overestimated. A release of enhanced B.C. fish, for example, at a time when they would interact with a large abundance of other sockeye, might not be beneficial. One effect is certain; the weight of catch generated from such releases will be smaller than normally assumed by the usual cost/benefit analyses. The current cyclical pattern of oscillation in minimum total ocean sockeye abundances of all ages shows low abundances to be about 50-60% of the highs (Fig. 15). More dramatic differences between highs and lows exist for other age groupings (e.g. Fig. 16). This pattern of abundances suggests that, if more recent data confirm findings here, we should explore the possibility of periodic releases of enhanced B.C. sockeye which are timed to utilize the ocean in years of low sockeye abundance. Fish from such releases should grow larger and yield more catch than fish released at times when numerous competitors will be present. Lake fertilization is the enhancement technique

which is most amenable to this type of approach. It is relatively inexpensive and flexible, and there are no large fixed costs which must be considered in the "off years". Such fixed costs may rule out the periodic light loading of sockeye spawning channels that would be needed for this pulsed release strategy. Because Bristol Bay sockeye constitute the largest proportion of the total sockeye in the Gulf of Alaska, attempts to focus B.C. fish releases in the low abundance period will have a relatively small effect on increasing total Gulf of Alaska abundance in those low years.

Lake enrichment can be used in a pulsed release strategy in practical management situations, even if cyclic dominance patterns change in Bristol Bay. For example, low escapements of Bristol Bay fish will be known in the fall of any year, which gives about a 6-month lead time before fertilization must be done in B.C. Such a release strategy is currently being investigated.

Finally, a concerted effort should be made to establish a formal international body to help monitor and coordinate enhancement efforts in various countries bordering the North Pacific Ocean, particularly since Alaska and British Columbia have plans for large-scale enhancement. This body could also fund and coordinate research on high seas interactions among salmonid stocks and it could be funded by imposing a tax on juveniles released as a result of enhancement programs. Those countries which contribute most to the problem by doing extensive enhancement will thus bear most of the cost. Without this international body to coordinate enhancement efforts in a number of countries, the incentive will remain for each country to continue adding enhancement facilities until there is no net profit gained, much like the problem of overcapitalization of fishing fleets (Crutchfield and Pontecorvo 1969). Hopefully, that is one mistake made in the past which we will not repeat on a broader scale.

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REFERENCES

Burgner, R.L., C.J. DiCostanzo, R.J. Ellis, G.Y. Harry, Jr., W.L. Hartman, O.E. Kerns, Jr., O.A. Mathisen, and W.F. Royce. 1969. Biological studies and estimates of optimum escapements of sockeye salmon in the major river systems in southwestern Alaska. Fish. Bull. (U.S.) 67 (2):405-459.

Cousens, N.B.F., G.A. Thomas, C.G. Swan, M.C. Healey. 1982. A review of salmon escapement estimation techniques. Can. Tech. Rep. Fish. Aquat. Sci. 1108:1-122.

Cushing, D.H. 1982. Climate and Fisheries. Academic Press, London, 373 p.

Crutchfield, J.A. and G. Pontecorvo. 1969. The Pacific Salmon Fisheries. A Study of Irrational Conservation. Baltimore, Johns Hopkins Press.

Davidson, F.A. and E. Vaughan. 1941. Relation of population size to marine growth and time of spawning migration in the pink salmon (Oncorhynchus gorbuscha) of southeastern Alaska. J. of Marine Research 4:231-246.

Foerster, R.E. 1944. The relation of lake population density to size of young sockeye salmon (Oncorhynchus nerka). J. Fish. Res. Board Can. 6:267-280.

Fredin, R.A., R.L. Major, R.G. Bakkala, and G.K. Tanonaka. 1977. Pacific salmon and the high seas salmon fisheries of Japan. Northwest and Alaska Fisheries Center Processed Report, Seattle, Wash., 324 pp.

French, R., H. Bilton, M. Osako and A.C. Hartt. 1976. Distribution and origin of sockeye salmon (Oncorhynchus nerka) in offshore waters of the North Pacific Ocean. Intl. N. Pacific Fish. Comm. Bull. 34, 113 pp.

French, R. and R.G. Bakkala. 1974. A new model of ocean migrations of Bristol Bay sockeye salmon. Fish. Bull. (U.S.), 72 (2):589-614.

Fry, F.E.J. 1949. Statistics of a lake trout fishery. Biometrics 5:27-67.

Godfrey, H. 1958. A comparison of sockeye catches at Rivers Inlet and Skeena River, B.C., with particular reference to age at maturity. J. Fish. Res. Board Can. 15:331-354

Godfrey, H. 1959. Variations in annual average weights of British Columbia pink salmon, 1944-1958. J. Fish. Res. Board Can. 16(3):329-337.

Gulland, J.A. 1965. Estimation of mortality rates. Annex to Arctic Fisheries Working Group Report. Intl. Council Explor. Sea, C.M. Document 3:1-9.

Hartt, A.C. 1980. Juvenile salmonids in the oceanic ecosystem--the critical first summer. In: W.J. McNeil and D.C. Himsworth (eds.). Salmonid Ecosystems of the North Pacific. Oregon State Univ. Press, Corvallis, Ore., p. 25-57.

Hartt, A.C. and M.B. Dell. In press. Migrations and growth of juvenile Pacific salmon and steelhead trout during their first summer in the open sea. Intl. North Pacific Fish. Comm. Bull.

Henry, K.A. 1961. Racial identification of Fraser River sockeye salmon by means of scales and its applications to salmon management. International Pacific Salmon Fisheries Commission, Bull. XII, 97 pp.

Jenkinson, D.W. and H.T. Bilton. 1973. Age composition of 1972 British Columbia sockeye, chum and pink salmon catches. Fish. Res. Board Can. Manuscript Report Series No. 1253, 101 pp.

Kadowaki, R. 1981. The Skeena River test fishery, 1955-1976. Unpubl. MS, Canada Dept. of Fisheries and Oceans, Prince Rupert, B.C. 37p.

Killick, S.R. and W.A. Clemens. 1963. The age, sex ratio and size of Fraser river sockeye salmon 1915 to 1960. Intl. Pacific Salmon Fish. Comm. Bull. XIV:1-140.

Larkins, H.A. 1964. Some epipelagic fishes of the North Pacific Ocean, Bering Sea, and Gulf of Alaska. Trans. Amer. Fish. Soc. 93:286-290.

LeBrasseur, R.J. 1966. Stomach contents of salmon and steelhead trout in the Northeastern Pacific Ocean. J. Fish. Res. Board Can. 23(1):85-100.

Manzer, J.I. 1968. Food of Pacific salmon and steelhead trout in the northeastern Pacific Ocean. J. Fish. Res. board Can. 25:1085-1089.

Mathews, S.B. 1980. Trends in Puget Sound and Columbia R. coho salmon. In: W.J. McNeil and D.C. Himsworth (ed.) Salmonid Ecosystems of the North Pacific. Oregon State University Press, Corvallis, Ore., p. 133-145.

Mysak, L.A., W.W. Hsieh and T.R. Parsons. 1982. On the relationship between interannual baroclinic waves and fish populations in the Northeast Pacific. Biol. Oceanog. 2(1):63-103.

National Bureau of Standards. 1952. Tables of the Binomial Probability Distribution. Applied Mathematics Series 6. U.S. Government Printing Office. Wash. D.C. 387 p.

Ott, L. 1977. An Introduction to Statistical Methods and Data Analysis. Duxbury Press, Mass. 730 p.

Parker, R.R. 1968. Marine mortality schedules of pink salmon of the Bella Coola River, central British Columbia. J. Fish. Res. Board Can. 25(4):757-794.

Parsons, R. 1974. Statistics for Decision Makers. Harper and Row, Publ., New York, 638 p.

Peterman, R.M. 1978. Testing for density-dependent marine survival in Pacific salmonids. J. Fish. Res. Board Can. 35:1434-1450.

Peterman, R.M. 1981. Form of random variation in salmon smolt-to-adult relations and its influence on production estimates. Can. J. Fish. Aquat. Sci. 38(9):1113-1119.

Peterman, R.M. 1982a. Nonlinear relation between smolts and adults in Babine Lake sockeye salmon (Oncorhynchus nerka) and implications for other salmon populations. Can. J. Fish. Aquat. Sci. 39:904-913.

Peterman, R.M. 1982b. Model of salmon age structure and its use in preseason forecasting and studies of marine survival. Can. J. Fish. Aquat. Sci. 39:1444-1452.

Peterman, R.M. 1984. Density-dependent growth in early ocean life of sockeye salmon (Oncorhynchus nerka). In press, Can. J. Fish. Aquat. Sci. 41:

Peterman, R.M. and F.Y.C. Wong. 1984. Cross correlations between reconstructed ocean abundances of Bristol Bay and British Columbia sockeye salmon (Oncorhynchus nerka). In press, Can. J. Fish. Aquat. Sci. 41:

Ricker, W.E. 1969. Effects of size-selective mortality and sampling bias on estimates of growth, mortality, production, and yield. J. Fish. Res. Board Can. 26:479-541.

Ricker, W.E. 1973. Linear regressions in fishery research. J. Fish. Res. Board Can. 30:409-434.

Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. 191:1-382.

Ricker, W.E. 1976. Review of rate of growth and mortality of Pacific salmon in salt water, and non-catch mortality caused by fishing. J. Fish. Res. Board Can. 33:1483-1524.

Ricker, W.E. 1979. Growth rates and models. In: W.S. Hoar, D.J. Randall and J.R. Brett (eds.). Fish Physiology. Academic Press, N.Y. Vol. 8: 677-743.

Ricker, W.E. 1982. Size and age of British Columbia sockeye salmon (Oncorhynchus nerka) in relation to environmental factors and the fishery. Can. Tech. Rep. Fish. Aquat. Sci. 1115:1-117.

Rigler, F.H. 1982. The relation between fisheries management and limnology. Trans. Amer. Fish. Soc. 111:121-132.

Rogers, D.E. 1973. Abundance and size of juvenile sockeye salmon, Oncorhynchus nerka, and associated species in Lake Aleknagik, Alaska, in relation to their environment. Fish. Bull. (U.S.) 71(4): 1061-1075.

Rogers, D.E. 1980. Density-dependent growth of Bristol Bay sockeye salmon. In W.J. McNeil and D.C. Himsworth (ed.) Salmonid Ecosystems of the North Pacific, Oregon State University Press, Corvallis, p. 267-283.

Todd, I. St. P. and P.A. Larkin. 1971. Gillnet selectivity on sockeye (Oncorhynchus nerka) and pink salmon (O. gorbuscha) of the Skeena River system, British Columbia. J. Fish. Res. Board Can. 28:821-842.

Ware, D.M. 1980. Bioenergetics of stock and recruitment. Can. J. Fish. Aquat. Sci. 37(6):1012-1024.

Yuen, H., B. Bue and C.P. Meacham. 1981. Bristol Bay sockeye salmon (O. nerka) age, weight, and length statistics, 1957-1977. Alaska Dept. Fish and Game, Tech. Data Rep. 67:1-155.

APPENDIX A

Appendix Table A1. Sockeye stocks included in the analysis of dependent variates such as body size, marine survival rates, etc. Sources of catch and escapement abundances, by age, are also shown.

BRITISH COLUMBIA

Stock	Abbreviation	Life History Type	Source
Adams River	Ad	sub-2	J. Roos & J. Woodey, IPSFC (pers. comm.)
Babine Lake	Ba	sub-2	E. Zyblut, D. Anderson R. Kadowaki, DFO (pers. comm.)
Chilko Lake	Ch	sub-2	J. Roos & J. Woodey, IPSFC (pers. comm.)
Cultus Lake	Cu	sub-2	J. Roos & J. Woodey, IPSFC (pers. comm.)
Owikeno Lake	Ow	sub-2	E. Zyblut, M. Farwell DFO (pers. comm.), age structure from Bilton et al. sampling program, see Peterman and Wong (1984)
Stellako River	St	sub-2	J. Roos & J. Woodey, IPSFC (pers comm.)

BRISTOL BAY, ALASKA

Stock	Abbreviation	Life History Type	Source
Branch R.	Br	sub-2, sub-3	K. Parker & C.P. Meacham, ADFG (pers. comm.)
Egegik R.	Eg	sub-2, sub-3	"
Igushik R.	Ig	sub-2, sub-3	"
Kvichak R.	Kv	sub-2, sub-3	"
Naknek R.	Na	sub-2, sub-3	"
Nuyakuk R.	Nuy	sub-2, sub-3	"
Snake R.	Sn	sub-2, sub-3	"
Togiak R.	Tog	sub-2, sub-3	"
Ugashik R.	Ug	sub-2, sub-3	"
Wood R.	Wo	sub-2, sub-3	"

Appendix Table A2. Dependent variables used with the sockeye stocks listed in Appendix Table A1, arranged alphabetically by salmon stock, within B.C. and Alaska. Abbreviations used are: MEF = mideye to fork of tail, PO-H = postorbital-hypural and T.F. = Skeena River test fishery.

BRITISH COLUMBIA

Stock	Variable Label	Variable Description
Adams - sub 2	Y17	Mean weight of 4_2s (kg) - U.S. purse seine
	Y19	4_2 Mean standard length (cm) on spawning grounds, males
	Y20	4_2 Mean standard length (cm) on spawning grounds, females
Babine - sub 2	Y1	Marine Survival Residuals - (corrected regression)
	Y2	Log_e (Adults/Smolt)
	Y3	4_2 Fork Length - (cm) - commercial gillnet samples
	Y4	5_2 Fork Length - (cm) - commercial gillnet samples
	Y5	4_2 Instantaneous Growth Rate from commercial gillnet samples
	Y6	5_2 Instantaneous Growth Rate from commercial gillnet samples
	Y8	Weighted Mean Age at Return (including jacks) for brood class
	Y9	Mean PO-H Length - 4_2 Males (cm) - T.F.
	Y10	Mean PO-H Length - 4_2 Females (cm) - T.F.
	Y11	Mean PO-H Length - 5_2 Males (cm) - T.F.
	Y12	Mean PO-H Length - 5_2 Females (cm) - T.F.
	Y13	4_2 Instantaneous growth rate - male - T.F.
	Y14	4_2 Instantaneous growth rate - female - T.F.
	Y15	5_2 Instantaneous growth rate - male - T.F.
	Y16	5_2 Instantaneous growth rate - female - T.F.
Chilko - sub 2	Y21	Marine Survival Residuals - (functional regression)
	Y2	Log_e (Adults/Smolt)
	Y17	Mean Weight of 4_2 (kg) - U.S. purse seine
	Y19	4_2 Mean standard length (cm) on spawning grounds, males
	Y20	4_2 Mean standard length (cm) on spawning grounds, females
Cultus - sub 2	Y19	4_2 Mean standard length (cm) on spawning grounds, males
	Y20	4_2 Mean standard length (cm) on spawning grounds, females
Owikeno - (River's Inlet) sub 2	Y3	4_2 Fork Length - (cm) - commercial gillnet samples
	Y4	5_2 Fork Length - (cm) - commercial gillnet samples
Stellako - sub 2	Y19	4_2 Mean standard length (cm) on spawning grounds, males
	Y20	4_2 Mean standard length (cm) on spawning grounds, females

Table A2 Continued.

ALASKA

Stock	Variable Label	Variable Description
Branch - sub 2	Y22	3_2 MEF Length - (mm) - escapement
	Y23	4_2 MEF Length - (mm) - escapement
	Y24	5_2 MEF Length - (mm) - escapement
Branch - sub 3	Y29	5_3 MEF Length - (mm) - escapement
	Y30	6_3 MEF Length - (mm) - escapement
Egegik - sub 2	Y34	4_2 MEF Length - (mm) - catch and escapement
	Y35	5_2 MEF Length - (mm) - catch and escapement
Egegik - sub 3	Y37	4_3 MEF Length - (mm) - catch and escapement
	Y38	5_3 MEF Length - (mm) - catch and escapement
	Y39	6_3 MEF Length - (mm) - catch and escapement
Igushik - sub 2	Y23	4_2 MEF Length - (mm) - escapement
	Y24	5_2 MEF Length - (mm) - escapement
Igushik - sub 3	Y29	5_3 MEF Length - (mm) - escapement
	Y30	6_3 MEF Length - (mm) - escapement
Kvichak - sub 2	Y22	3_2 MEF Length - (mm) - escapement
	Y23	4_2 MEF Length - (mm) - escapement
	Y24	5_2 MEF Length - (mm) - escapement
	Y25	3_2 Instantaneous Growth Rate
	Y26	4_2 Instantaneous Growth Rate
	Y27	5_2 Instantaneous Growth Rate
	Y28	Weighted Mean Age at return for brood class
Kvichak - sub 3	Y29	5_3 MEF Length - (mm) - escapement
	Y30	6_3 MEF Length - (mm) - escapement
	Y31	5_3 Instantaneous Growth Rate
	Y32	6_3 Instantaneous Growth Rate
	Y28	Weighted Mean Age at return for brood class
Naknek - sub 2	Y21	Marine Survival Residuals - (functional regression)
	Y2	Log_e (Adults/Smolt)
	Y22	3_2 MEF Length - (mm) - escapement
	Y23	4_2 MEF Length - (mm) - escapement
	Y24	5_2 MEF Length - (mm) - escapement
	Y25	3_2 Instantaneous Growth Rate
	Y26	4_2 Instantaneous Growth Rate
	Y27	5_2 Instantaneous Growth Rate
	Y28	Weighted Mean Age at return for brood class

Table A2 Continued.

Stock	Variable Label	Variable Description
Naknek - sub 3	Y21	Marine Survival Residuals - (functional regression)
	Y2	Log_e (Adults/Smolt)
	Y29	5_3 MEF Length - (mm) - escapement
	Y30	6_3 MEF Length - (mm) - escapement
	Y31	5_3 Instantaneous Growth Rate
	Y32	6_3 Instantaneous Growth Rate
	Y28	Weighted Mean Age at return for brood class
Nuyakuk - sub 2	Y23	4_2 MEF Length - (mm) - escapement
	Y24	5_2 MEF Length - (mm) - escapement
Nuyakuk - sub 3	Y29	5_3 MEF Length - (mm) - escapement
	Y30	6_3 MEF Length - (mm) - escapement
Snake - sub 2	Y23	4_2 MEF Length - (mm) - escapement
	Y24	5_2 MEF Length - (mm) - escapement
Snake - sub 3	Y29	5_3 MEF Length - (mm) - escapement
	Y30	6_3 MEF Length - (mm) - escapement
Togiak - sub 2	Y34	4_2 MEF Length - (mm) - catch and escapement
	Y35	5_2 MEF Length - (mm) - catch and escapement
	Y36	6_2 MEF Length - (mm) - catch and escapement
Togiak - sub 3	Y38	5_3 MEF Length - (mm) - catch and escapement
	Y39	6_3 MEF Length - (mm) - catch and escapement
Ugashik - sub 2	Y21	Marine Survival Residuals - (functional regression)
	Y2	Log_e (Adults/Smolt)
	Y28	Weighted Mean Age at return for brood class
	Y33	3_2 MEF Length - (mm) - catch and escapement
	Y34	4_2 MEF Length - (mm) - catch and escapement
	Y35	5_2 MEF Length - (mm) - catch and escapement
	Y40	3_2 Instantaneous Growth Rate - catch and escapement
	Y41	4_2 Instantaneous Growth Rate - catch and escapement
	Y42	5_2 Instantaneous Growth Rate - catch and escapement
Ugashik - sub 3	Y21	Marine Survival Residuals - (functional regression)
	Y2	Log_e (Adults/Smolt)
	Y28	Weighted Mean Age at return for brood class
	Y37	4_3 MEF Length - (mm) - catch and escapement
	Y38	5_3 MEF Length - (mm) - catch and escapement
	Y39	6_3 MEF Length - (mm) - catch and escapement
	Y43	4_3 Instantaneous Growth Rate - catch and escapement
	Y44	5_3 Instantaneous Growth Rate - catch and escapement
	Y45	6_3 Instantaneous Growth Rate - catch and escapement

Table A2 Continued.

Stock	Variable Label	Variable Description
Wood - sub 2	Y22	3_2 MEF Length - (mm) - escapement
	Y23	4_2 MEF Length - (mm) - escapement
	Y24	5_2 MEF Length - (mm) - escapement
Wood - sub 3	Y29	5_3 MEF Length - (mm) - escapement
	Y30	6_3 MEF Length - (mm) - escapement

Appendix Table A3. Detailed descriptions of dependent variates, number of stocks, and sources of data, arranged in sequence of variable name.

Variable Label	Variable Description	Stocks	# of Stocks	Source
Y1	Residuals in marine survival from smolt-to-adult relation (corrected regression fit)	Babine	1	Peterman, 1982a
Y2	Natural logarithm of number of adult returns per smolt (sub-2 and sub-3 for Alaskan stocks)	Babine, Chilko Naknek Ugashik	6	Peterman, 1982a Woodey, IPSFC (pers. comm) Yuen et al., 1981
Y3	Mean fork length of age 4_2 returns from commercial gillnet samples - (cm)	Babine, Owikeno	2	Ricker, 1982
Y4	Mean fork length of age 5_2 returns from commercial gillnet samples - (cm)	Babine, Owikeno	2	Ricker, 1982
Y5	Instantaneous growth rate of smolts to age 4_2 from commercial gillnet samples	Babine	1	Kadowaki, 1981 Peterman, 1978
Y6	Instantaneous growth rate of smolts to age 5_2 from commercial gillnet samples	Babine	1	Kadowaki, 1981 Peterman, 1978
Y8	Weighted mean age at return with jacks included, by brood year	Babine	1	Peterman, 1978
Y9	Mean postorbital-hypural length of male age 4_2 returns from the Skeena R. test fishery - (cm)	Babine	1	Kadowaki, 1981
Y10	Mean postorbital-hypural length of female age 4_2 returns from the Skeena R. test fishery - (cm)	Babine	1	Kadowaki, 1981
Y11	Mean postorbital-hypural length of male age 5_2 returns from the Skeena R. test fishery - (cm)	Babine	1	Kadowaki, 1981

Table A3 Continued.

Variable Label	Variable Description	Stocks	# of Stocks	Source
Y12	Mean postorbital-hypural length of female age 5_2 returns from the Skeena R. test fishery - (cm)	Babine	1	Kadowaki, 1981
Y13	Instantaneous growth rate of smolts to age 4_2 males from the Skeena R. test fishery - (postorbital-hypural length)	Babine	1	From Y9 and smolts from Kadowaki, 1981
Y14	Instantaneous growth rate of smolts to age 4_2 females from the Skeena R. test fishery - (postorbital-hypural length)	Babine	1	From Y10 and smolts from Kadowaki, 1981
Y15	Instantaneous growth rate of smolts to age 5_2 males from the Skeena R. test fishery - (postorbital-hypural length)	Babine	1	From Y11 and smolts from Kadowaki, 1981
Y16	Instantaneous growth rate of smolts to age 5_2 females from the Skeena R. test fishery - (postorbital-hypural length)	Babine	1	From Y12 and smolts from Kadowaki, 1981
Y17	Mean weight of age 4_2 returns captured by U.S. purse seines - (kg)	Adams, Chilko	2	Woodey, IPSFC (pers. comm.)
Y19	Mean standard length of 4_2 males on spawning grounds - (cm)	Adams, Chilko, Cultus Stellako	4	Woodey, IPSFC (pers. comm.)
Y20	Mean standard length of 4_2 females on spawning grounds - (cm)	Adams, Chilko, Cultus Stellako	4	Woodey, IPSFC (pers. comm.)
Y21	Residuals in marine survival from smolt-to-adult relation (functional regression fit) (sub-2 and sub-3 for Alaskan stocks)	Chilko Naknek Ugashik	5	Peterman, 1978 Yuen et al., 1981
Y22	Mean mideye-to-fork-of-tail length for age 3_2 adults from the escapement - (mm)	Branch, Kvichak, Naknek Wood	4	Yuen et al., 1981

Table A3 Continued.

Variable Label	Variable Description	Stocks	# of Stocks	Source
Y23	Mean mideye-to-fork-of-tail length for age 4_2 adults from the escapement - (mm)	Branch, Igushik, Kvichak Naknek, Nuyakuk Snake, Wood	7	Yuen et al., 1981
Y24	Mean mideye-to-fork-of-tail length for age 5_2 adults from the escapement - (mm)	Branch, Igushik, Kvichak Naknek, Nuyakuk, Snake, Wood	7	Yuen et al., 1981
Y25	Instantaneous growth rate of smolts to age 3_2 adults from the escapement -(mideye to fork-of-tail)	Kvichak, Naknek	2	From Y33 and smolts from Meacham (pers. comm.)
Y26	Instantaneous growth rate of smolts to age 4_2 adults from the escapement - (mideye to fork-of-tail)	Kvichak Naknek	2	From Y23 and smolts from Meacham
Y27	Instantaneous growth rate of smolts to age 5_2 adults from the escapement - (mideye to fork-of-tail)	Kvichak, Naknek	2	From Y24 and smolts from Meacham (pers. comm.)
Y28	Weighted mean age of adults at return (sub-2 and sub-3 for Alaskan stocks) by brood year	Kvichak Naknek Ugashik	6	Yuen et al., 1981
Y29	Mean mideye-to-fork-of-tail length for age 5_3 adults from the escapement - (mm)	Branch, Igushik, Kvichak Naknek, Nuyakuk Snake, Wood	7	Yuen et al., 1981
Y30	Mean mideye-to-fork-of-tail length for 6_3 adults from the escapement - (mm)	Branch, Igushik, Kvichak Naknek, Nuyakuk Snake, Wood	7	Yuen et al., 1981
Y31	Instantaneous growth rate of smolts to age 5_3 adults from the escapement - (mideye to fork-of-tail)	Kvichak, Naknek	2	From Y29 and smolts from Meacham (pers. comm.)

Table A3 Continued.

Variable Label	Variable Description	Stocks	# of Stocks	Source
Y32	Instantaneous growth rate of smolts to age 6_3 adults from the escapement - (mideye to fork-of-tail)	Kvichak Naknek	2	From Y30 and smolts from Meacham (pers. comm.)
Y33	Mean mideye to-fork-of-tail length for age 3_2 adults from the catch and escapement - (mm)	Ugashik	1	Yuen et al., 1981
Y34	Mean mideye-to-fork-of-tail length for age 4_2 adults from the catch and escapement - (mm)	Egegik, Togiak Ugashik	3	Yuen et al., 1981
Y35	Mean mideye-to-fork-of-tail length for age 5_2 adults from the catch and escapement - (mm)	Egegik, Togiak Ugashik	3	Yuen et al., 1981
Y36	Mean mideye-to-fork-of-tail length for age 6_2 adults from the catch and escapement - (mm)	Togiak	1	Yuen et al., 1981
Y37	Mean mideye-to-fork-of-tail length for age 4_3 adults from the catch and escapement - (mm)	Egegik Ugashik	2	Yuen et al., 1981
Y38	Mean mideye-to-fork-of-tail length for age 5_3 adults from the catch and escapement - (mm)	Egegik Togiak Ugashik	3	Yuen et al., 1981
Y39	Mean mideye-to-fork-of-tail length for age 6_3 adults from the catch and escapement - (mm)	Egegik Togiak Ugashik	3	Yuen et al., 1981
Y40	Instantaneous growth rate of smolts to age 3_2 adults from the catch and escapement - (mideye to fork-of-tail)	Ugashik	1	From Y33 and smolts from Meacham (pers. comm.)
Y41	Instantaneous growth rate of smolts to age 4_2 adults from the catch and escapement - (mideye to fork-of-tail)	Ugashik	1	From Y34 and smolts from Meacham (pers. comm.)

Table A3 Continued.

Variable Label	Variable Description	Stocks	# of Stocks	Source
Y42	Instantaneous growth rate of smolts to age 5_2 adults from the catch and escapement - (mideye to fork-of-tail)	Ugashik	1	From Y35 and smolts from Meacham (pers. comm.)
Y43	Instantaneous growth rate of smolts to age 4_3 adults from the catch and escapement - (mideye to fork-of-tail)	Ugashik	1	From Y37 and smolts from Meacham (pers. comm.)
Y44	Instantaneous growth rate of smolts to age 5_3 adults from the catch and escapement - (mideye to fork-of-tail)	Ugashik	1	From Y38 and smolts from Meacham (pers. comm.)
Y45	Instantaneous growth rate of smolts to age 6_3 adults from the catch and escapement - (mideye to fork-of-tail)	Ugashik	1	From Y39 and smolts from Meacham (pers. comm.)

APPENDIX B

Body Size of Babine Lake Sockeye

Adult body size data for Babine Lake sockeye are available from two sources, commercial gillnet catch samples and test fishery samples taken upstream from commercial gillnets. The two time series of data only overlap in 5 years.

Because commerical gillnet body sizes per fish might be a biased sample of sizes in the total recruit population, Skeena River test fishery data are used in combination with the catch data to derive an estimate of body size of recruits before gillnet harvest. It is then possible to determine for those 5 years if body sizes from commercial or test fishery samples are well correlated with body sizes of recruits prior to the onset of fishing. Skeena River sockeye include sub-2 as well as sub-3 fish but only sub-2 data are relevant to Babine Lake sockeye. Annual mean body size of recruits, by age and sex, is estimated by taking a weighted average of body sizes sampled in the gillnet catch and test fisheries, where weighting is by abundance:

$$S_R = \frac{(S_C \times N_C) + (S_T \times N_U)}{N_C + N_U}$$

where:

S_R = annual mean body size (cm) of recruits, by age and sex

S_C = annual mean body size (cm) of fish in gillnet catch, by age and sex

S_T = annual mean body size (cm) fish in test fishery catch, by age and sex

N_C = annual number of Babine Lake sockeye caught in commercial gillnets, by age and sex.

N_U = annual number of Babine Lake sockeye escaping upriver of commercial fisheries. Included in this are Indian catches plus escapement.

N_C by age and sex is calculated by taking known catches by age (Zyblut, Anderson and Kadowaki, DFO, Prince Rupert, pers. comm.) and partitioning them by sex according to data in Kadowaki (1981, Table 10). The escapement component of N_U is similarly calculated from known escapements (Zyblut et al.)

and Kadowaki's Table 10 sex ratios. Indian catches, which are generally less than 3% of the annual run (Zyblut et al.) are assumed to be 50% male. S_C and S_T are from Kadowaki (1981, Table 11). So for each sex-age group (4_2, 5_2 males and 4_2, 5_2 females) there are three size measures, S_R, S_C and S_T. S_T and S_C are correlated with S_R to see which gives the best approximation to the size of recruits, S_R (H_o:r = 0). Because of limited test fishery and commercial size data, the time series overlap is only from 1967 through 1971.

Results below are for n = 5:

	4_2 males		4_2 females		5_2 males		5_2 females	
variates	r	P	r	P	r	P	r	P
$S_C - S_R$	0.80	0.10	0.87	0.055	0.86	0.062	0.88	0.048*
$S_T - S_R$	0.98	0.004*	0.97	0.005*	0.902	0.036*	0.93	0.023*
$S_C - S_T$	0.68	0.21	0.80	0.10	0.57	0.32	0.66	0.22

The Skeena River test fishery data thus provide the best estimate of the body size of recruits. All correlation coefficients for that relation between size of recruits and size of test fish samples are significant and are greater than 0.9. The commercial size data are not quite as good, especially for 4_2 males, perhaps because of the selectivity of commercial gillnets for fish in an intermediate size range (Todd and Larkin 1971). These results are not caused by most of the population escaping the commercial nets; the exploitation rate has averaged about 50-60% per year.

Because of the high correlation between S_T and S_R, and because S_R could only be calculated for 5 years, the longer time series of test fishery size data is used in the analysis of Gulf of Alaska stock interactions, along with the existing commercial size sample data. Annual average body sizes for S_T are generated from raw data provided by R. Kadowaki (DFO, Prince Rupert) for years 1977 - 1981 (1980 data are missing) and used these, along with Kadowaki's (1981) figures (his Table 11). These Y variates are denoted Y9 - Y12, in the multiple regression analyses, as opposed to Y3 - Y6 which are

based only on gillnet size data. The test fishery size data thus cover 1966 through 1981 with 1972 and 1980 missing.

Instantaneous growth rates from smolts to adults are also calculated from smolt size and these test fishery growths and are denoted Y13 - Y16.

Table 1. Correlation coefficients between ocean abundance of a given stock, by age, and total Gulf of Alaska sockeye abundance of that same age. Sample sizes (number of years) are in parentheses. Underlined correlations indicate that the high values may be a result of a single extreme outlier point.

B.C. STOCKS

	AGES							
Stocks	2	3	4	5	2+3	4+5	> 2	All ages
Adams	.05 (17)	-.10 (17)	-.11 (18)	-.11 (17)	-.21 (17)	-.17 (18)	-.32 (17)	-.05 (17)
Babine	-.23 (17)	-.32 (17)	-.32 (17)	-.33 (17)	-.45 (17)	-.37 (16)	-.52* (15)	-.41 (15)
Chilko	.31 (17)	0.0 (17)	.01 (18)		-.14 (17)		-.23 (17)	-.28 (17)
Cultus	-.05 (17)	-.25 (17)	-.26 (18)	-.14 (15)	-.05 (17)	-.33 (18)	-.32 (17)	.01 (17)
Owikeno	-.07 (17)	-.29 (17)	-.30 (18)	-.25 (19)	-.53* (17)	-.45 (18)	-.57* (17)	-.31 (17)
Stellako	.04 (17)	-.18 (17)	-.19 (18)	.02 (19)	-.27 (17)	-.34 (18)	-.34 (17)	.01 (17)

* $P < .05$
** $P < .01$

(See next page for Alaskan stocks)

Table 1 Continued.

ALASKAN STOCKS

	AGES								
Stocks	2	3	4	5	6	2+3	4+5	>2	All ages
Branch	.86** (17)	.43 (17)	.43 (18)	.18 (19)	.02 (20)	.52* (17)	.32 (18)	.27 (17)	.32 (17)
Egegik	.93** (17)	.92** (17)	.91** (18)	.88** (19)	.93** (20)	.91** (17)	.90** (18)	.83** (17)	.78** (17)
Igushik	.34 (17)	.33 (17)	.33 (18)	.26 (19)	.21 (20)	.51* (17)	.42 (18)	.38 (17)	.42 (17)
Kvichak	.94** (17)	.98** (17)	.98** (18)	.99** (19)		.98** (17)	.99** (18)	.99** (17)	.98** (17)
Naknek	.50* (17)	.61** (17)	.59** (18)	.33 (19)		.64** (17)	.63** (18)	.75** (17)	.64** (17)
Nuyakuk	.23 (17)	.59* (17)	.58* (18)	.50* (19)	.12 (20)	.51* (17)	.56* (18)	.56* (17)	.32 (17)
Snake	-.07 (17)	-.06 (17)	-.07 (18)	.04 (19)	-.16 (20)	.10 (17)	-.15 (18)	-.04 (17)	-.03 (17)
Togiak	.24 (17)	.63** (17)	.62** (18)	.53* (19)	.43 (20)	.70** (17)	.74** (18)	.75** (17)	.58** (17)
Ugashik	.85** (17)	.72** (17)	.72** (18)	.70** (19)		.85** (17)	.78** (18)	.76** (17)	.76** (17)
Wood	.02 (17)	.26 (18)	.25 (18)	.43 (19)	.26 (20)	.33 (17)	.31 (18)	.32 (17)	.31 (17)

* P <.05
** P <.01

Table 2. Summary of multiple regression statistics for British Columbia sockeye stocks. Headings for different ocean residence years (ORY=OEY, OEY+1, etc.) indicate which period during the ocean life is being examined (see text). Only statistics concerning the effect of total Gulf of Alaska sockeye abundance are summarized here (H_0:b_2=0). Probability shown is the probability that the stated number of significant cases of b_2 (at α=0.05) would have resulted by chance alone from the total number of tests performed. Probabilities in the first 9 columns are obtained from tables of the binominal probability distribution. Probabilities for the last column are obtained from the normal approximation method because no tables are available for such large samples. Instances with a high percentage of significant cases with probabilities less than 0.05 are noted with *.

British Columbia Stocks

Age category for X_1 and X_2 abundance variates

	2	3	4	5	6	2+3	4+5	>2	All	Sum
ORY=OEY										
Sum signif.b_2	3	2	0	2		0	4	4	3	18
Sum tests done	29	29	29	29	0	29	29	29	29	232
% tests signif.	10.3	6.9	0	6.9		0	13.8	13.8	10.3	7.8
Probability	0.12	0.25	0.23	0.25		0.23	0.041*	0.041*	0.12	0.019*
ORY=OEY+1										
Sum signif.b_2	3	3	2	4		9	1	0	0	22
Sum tests done	29	29	29	29	0	29	29	29	29	232
% tests signif.	10.3	10.3	6.9	13.8		31.0	3.4	0.0	0.0	9.5
Probability	0.12	0.12	0.25	0.041*		< .001*	0.34	0.23	0.23	<.001*
ORY=OEY+2										
Sum signif.b_2	3	3	3	0		2	2	2	2	17
Sum tests done	29	29	29	29	0	29	29	29	29	232
% tests signif.	10.3	10.3	10.3	0.0		6.9	6.9	6.9	6.9	7.3
Probability	0.12	0.12	0.12	0.23		0.25	0.25	0.25	0.25	0.024*
ORY=OEY+3										
Sum signif.b_2	0	0	0	0		0	1	0	0	1
Sum tests done	7	7	7	7	0	7	7	7	7	56
% tests signif.	0.	0.	0.	0.		0.	14.3	0.	0.	1.8
Probability	0.7	0.7	0.7	0.7		0.7	0.26	0.7	0.7	0.17

Table 3. Same as Table 2 except for sub-2 Bristol Bay sockeye.

Bristol Bay Stocks - sub-2

Age category for X_1 and X_2 abundance variates

	2	3	4	5	6	2+3	4+5	> 2	All	Sum
ORY=OEY										
Sum signif. b_2	0	3	0	2	2	5	2	3	8	25
Sum tests done	42	42	42	42	42	42	42	42	42	378
% tests signif.	0.	7.1	0.0	4.8	4.8	11.9	4.8	7.1	19.0	6.6
Probability	0.12	0.19	0.12	0.28	0.28	0.04*	0.28	0.19	< .001*	0.033*
ORY=OEY+1										
Sum signif. b_2	2	5	2	2	2	4	1	3	6	27
Sum tests done	42	42	42	42	42	42	42	42	42	378
% tests signif.	4.8	11.9	4.8	4.8	4.8	9.5	2.4	7.1	14.3	7.1
Probability	0.28	0.04*	0.28	0.28	0.28	0.10	0.26	0.19	0.013*	0.015*
ORY=OEY+2										
Sum signif. b_2	0	0	4	2	1	1	3	2	3	16
Sum tests done	33	33	34	34	34	33	34	33	33	301
% tests signif.	0.	0.	11.8	5.9	2.9	3.0	8.8	6.1	9.1	5.3
Probability	0.18	0.18	0.06	0.27	0.32	0.32	0.15	0.27	0.15	0.10
ORY=OEY+3										
Sum signif.b_2	1	1	0	1	0	2	1	0	0	6
Sum tests done	12	12	13	13	13	12	13	12	12	112
%tests signif.	8.3	8.3	0.	7.7	0.	16.7	7.7	0.	0.	5.4
Probability	0.34	0.34	0.51	0.35	0.51	0.10	0.35	0.54	0.54	0.17

Table 4. Same as Table 2 except for sub-3 Bristol Bay sockeye stocks.

Bristol Bay Stocks - sub-3

Age category for X_1 and X_2 abundance variates

	2	3	4	5	6	2+3	4+5	>2	All	Sum
ORY=OEY										
Sum signif. b_2	3	2	1	2	1	0	6	5	4	24
Sum tests done	36	36	36	36	36	36	36	36	36	324
% tests signif.	8.3	5.6	2.8	5.6	2.8	0.	16.7	13.9	11.1	7.4
Probability	0.16	0.28	0.30	0.28	0.30	0.16	< .01*	0.024*	0.07	0.014*
ORY=OEY+1										
Sum signif. b_2	0	1	2	0	2	0	2	2	3	12
Sum tests done	36	36	36	36	36	36	36	36	36	324
% tests signif.	0.	2.8	5.6	0.	5.6	0.	5.6	5.6	8.3	3.7
Probability	0.16	0.30	0.28	0.16	0.28	0.16	0.28	0.28	0.16	0.057
ORY=OEY+2										
Sum signif. b_2	1	0	2	2	0	0	2	2	2	11
Sum tests done	31	31	33	33	33	31	33	31	31	287
% tests signif.	3.2	0.	6.1	6.1	0.	0.	6.1	6.5	6.5	3.8
Probability	0.33	0.20	0.27	0.27	0.18	0.20	0.27	0.26	0.26	0.071
ORY=OEY+3										
Sum signif. b_2	1	1	0	0	0	1	0	0	1	4
Sum tests done	12	12	12	13	13	12	12	12	12	110
% tests signif.	8.3	8.3	0.	0.	0.	8.3	0.	0.	8.3	3.6
Probability	0.34	0.34	0.54	0.51	0.51	0.34	0.54	0.54	0.34	0.14

Table 5. Parameter estimates for equation (1) for all relations which have significant slopes (at α =0.05) on Gulf of Alaska sockeye abundance, X_2, within the important lags and age categories, as defined in text. Smolt age indicates which smolt life history type, sub-2 or sub-3. Lag indicates whether the analysis is for ocean residence yr (ORY) = ocean entry yr (OEY) or OEY+1. More detailed descriptions of each Y variate can be found in Appendix A, Table A3, using the Y variate labels such as Y20, Y19, etc. shown here in the fifth column. X age shows the age category for X_1 and X_2 abundances. Yrs = sample size. Parameter estimates are for regressions which used X_1 and X_2 abundances in millions of fish. Probabilities are shown for the two hypothesis tests on the slopes. * indicates that the value of the slope is suspect because of a single extreme point at high abundance.

Case no.	Stock	Smolt Age	Lag	Y variate	X Age	Yrs	Parameter estimates (raw values) a	b_1	b_2	$P_{b_1=0}$	$P_{b_2=0}$	Mult. r^2	Fig. no.
Body size as affected by abundance of young ages													
1	Chilko	2	1	Y20 4_2 female standard length (cm)	2+3	17	54.83	-0.4593	-0.0347	0.046	0.009	0.46	2
2	Chilko	2	1	Y19 4_2 male standard length (cm)	2+3	17	57.29	-0.4606	-0.0371	0.042	0.005	0.50	-
3	Chilko	2	1	Y17 4_2 weight (kg)	2+3	4	3.538	-0.2735	-0.0066	0.036	0.040	0.99	-
4	Stellako	2	1	Y20 4_2 female standard length (cm)	2+3	17	52.87	-0.2624	-0.0301	0.638	0.016	0.35	3
5	Stellako	2	1	Y19 4_2 male standard length (cm)	2+3	17	55.07	-0.3967	-0.0222	0.39	0.027	0.30	-
6	Owikeno	2	1	Y4 5_2 fork length (cm)	2+3	15	63.50	0.0576	-0.0364	0.82	0.036	0.42	4
7	Babine	2	1	Y4 5_2 fork length gillnet samples (cm)	2+3	15	64.90	0.1437	-0.0366	0.63	0.005	0.56	5
8	Babine	2	1	Y6 Inst. growth rate to 5_2 (gillnet)	2+3	12	2.198	-0.0199	-0.0011	0.22	0.025	0.45	6
9	Babine	2	1	Y16 Inst. growth rate to 5_2 female (test fishery)	2+3	8	1.981	-0.0178	-0.0010*	0.009	0.008	0.85	-

Table 5 Continued.

Case no.	Stock	Smolt Age	Lag	Y variate	X Age	Yrs	Parameter estimates (raw values) a	b_1	b_2	$P_{b_1=0}$	$P_{b_2=0}$	Mult. r^2	Fig. no.
10	Wood	2	1	Y24 5_2 fork length (mm)	3	15	571.25	-2.040	-0.238	0.40	0.031	0.41	7
11	Egegik	2	1	Y35 5_2 fork length (mm)	3	17	586.3	3.076	-0.5738	0.21	0.025	0.48	8
12	Wood	2	1	Y22 3_2 fork length (mm)	3	7	402.53	-66.30	2.1647*	0.046	0.035	0.74	-
13	Togiak	2	1	Y34 4_2 fork length (mm)	3	11	525.83	-28.72	0.2203	0.037	0.030	0.50	-
- - - Body size as affected by abundance of older ages - - -

Table 5 Continued.

Case no.	Stock	Smolt Age	Lag	Y variate	X Age	Yrs	Parameter estimates (raw values) a	b_1	b_2	$P_{b_1=0}$	$P_{b_2=0}$	Mult. r^2	Fig. no.
23	Ugashik	3	0	Y44 5_3 inst. growth rate	4+5	14	1.564	0.0266	-0.0018	0.08	0.034	0.35	11
24	Ugashik	3	0	Y45 6_3 inst. growth rate	4+5	14	1.666	0.0315	-0.0018	0.020	0.015	0.44	-
25	Naknek	3	0	Y30 6_3 fork length (mm)	4+5	17	563.85	-1.029	0.2362	0.64	0.039	0.37	-
26	Naknek	3	0	Y31 5_3 inst. growth rate	4+5	15	1.524	-0.0269	0.0011	0.023	0.033	0.37	-
27	Nuyakuk	3	0	Y29 5_3 fork length (mm)	>2	12	549.53	38.44	-0.9147	0.11	0.010	0.56	-
28	Ugashik	3	0	Y38 5_3 fork length (mm)	>2	17	545.41	4.232	-0.4365	0.17	0.030	0.30	12
29	Egegik	3	0	Y38 5_3 fork length (mm)	>2	17	533.00	2.516	-0.3820	0.14	0.045	0.27	-
30	Naknek	3	0	Y30 6_3 fork length (mm)	>2	16	584.20	-5.416	0.2830	0.07	0.031	0.31	-
31	Naknek	3	0	Y32 6_3 inst. growth rate	>2	15	1.644	-0.0202	0.0014	0.14	0.025	0.37	-
- - - - -	Mean age at return - - - - -

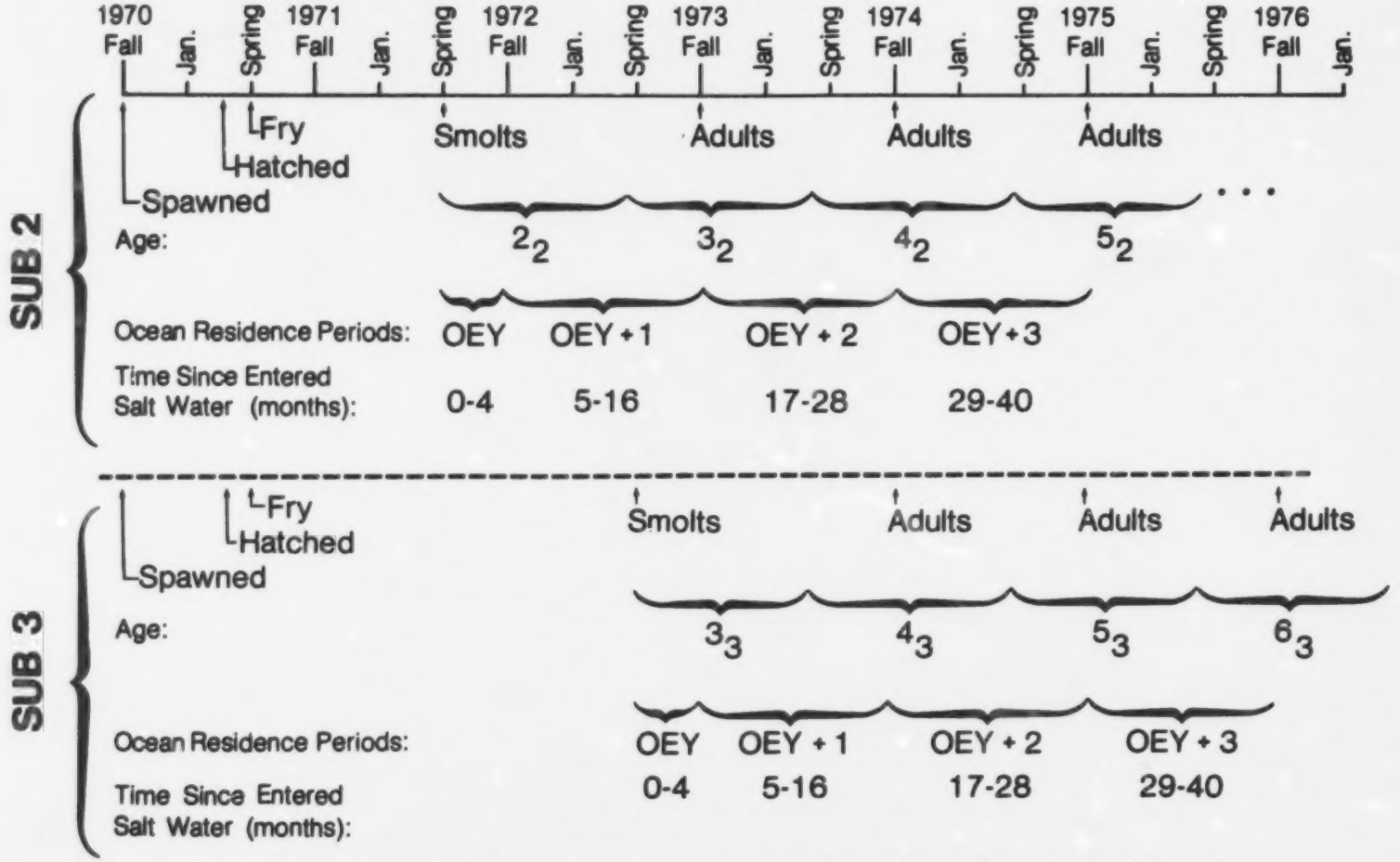

Fig. 1. Life history of sockeye salmon and the periods covered by the analyses of different ocean residence times. Top half illustrates a sub-2 stock in which smolts go to sea during their second year of life; bottom half is for a sub-3 stock.

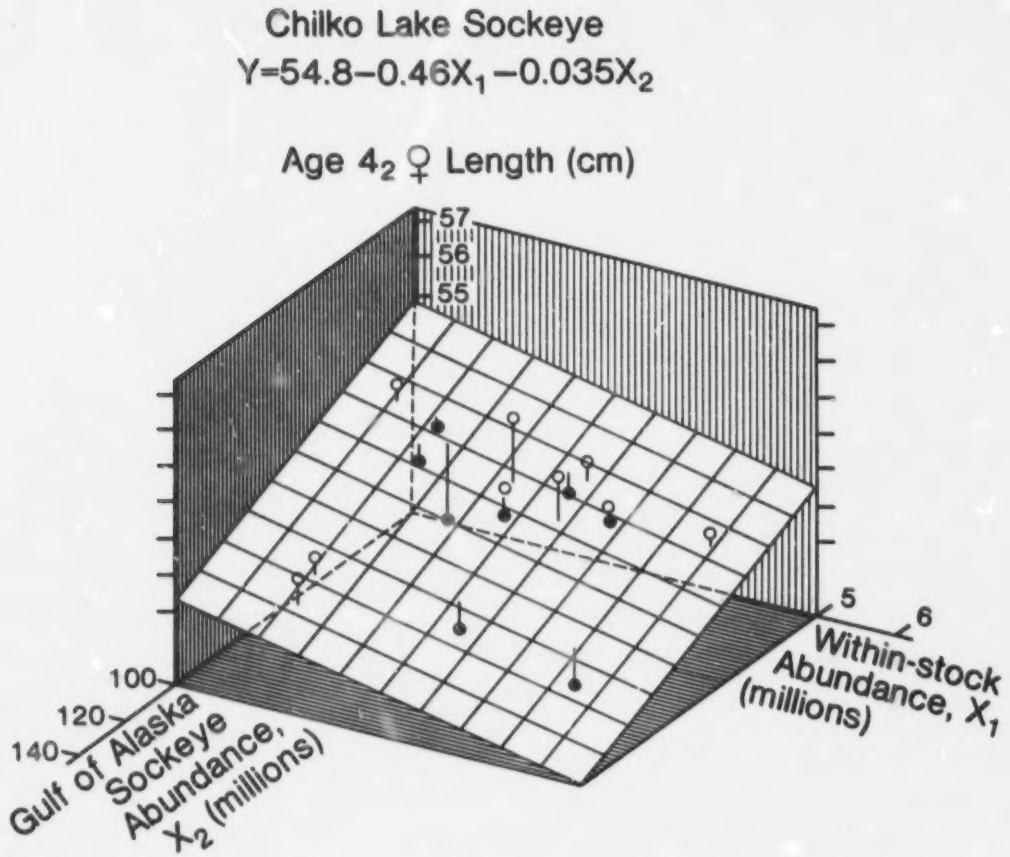

Fig. 2. Regression plane showing for Chilko L. sockeye salmon the relation between female age 4_2 standard length and the two independent variates, X_1 and X_2. X_1 is ocean abundance of ages 2 and 3 Chilko Lake fish (within-stock abundance) and X_2 is ocean abundance of ages 2 and 3 sockeye summed across all B.C. and Bristol Bay stocks (Gulf of Alaska sockeye abundance). Bottom back corner of the box is zero on both abundance axes. The 17 years of observed data are shown in relation to the regression plane by open circles (positive residuals) and solid circles (negative residuals). Detailed statistics are in Table 5.

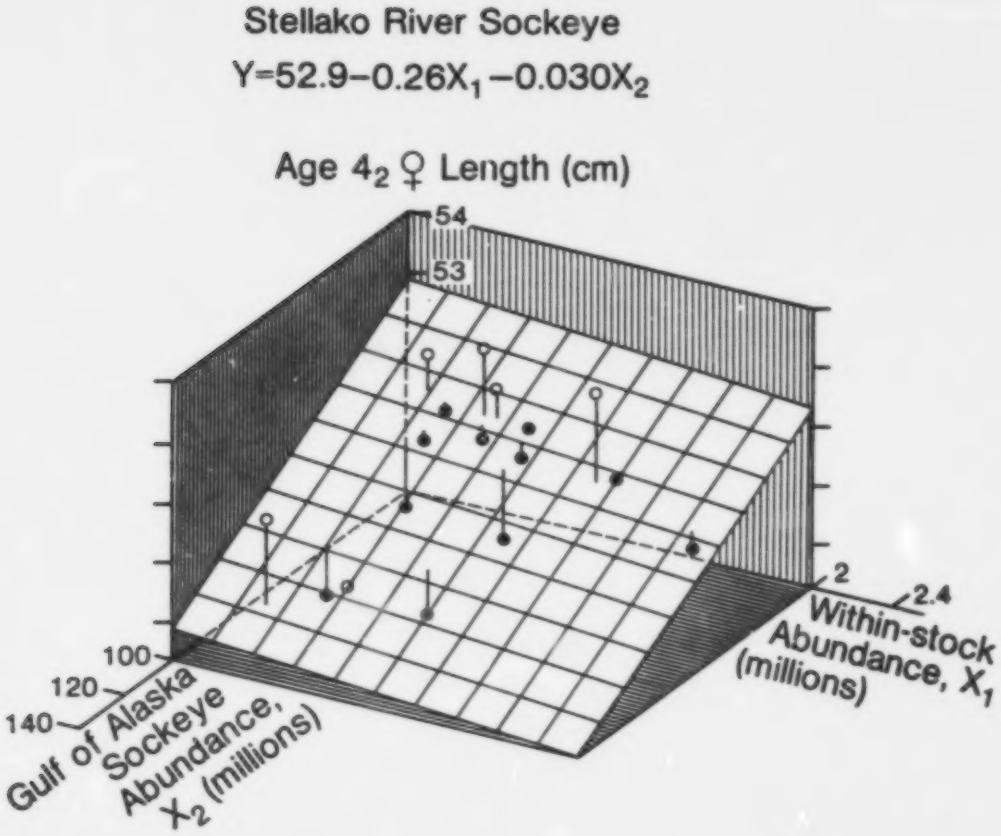

Fig. 3. Same as Fig. 2 except for Stellako R. sockeye salmon.

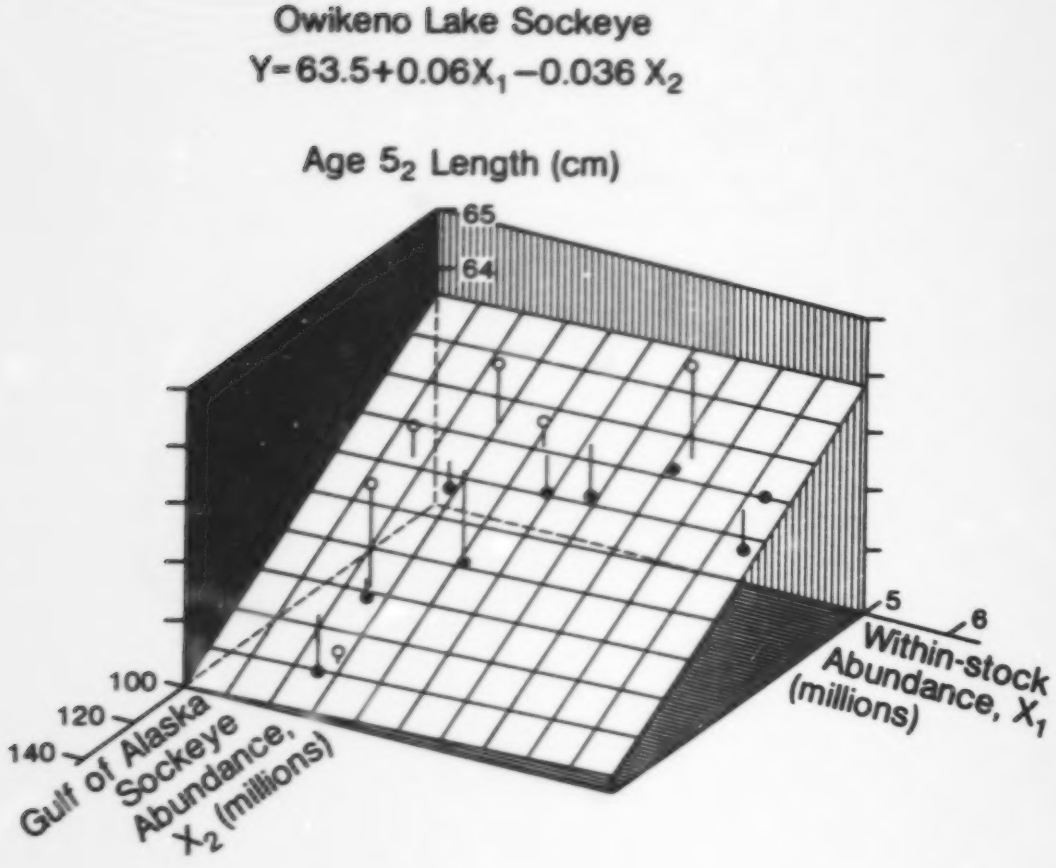

Fig. 4. Same as Fig. 2 except dependent variate is age 5_2 length (sexes combined) of Owikeno Lake sockeye salmon.

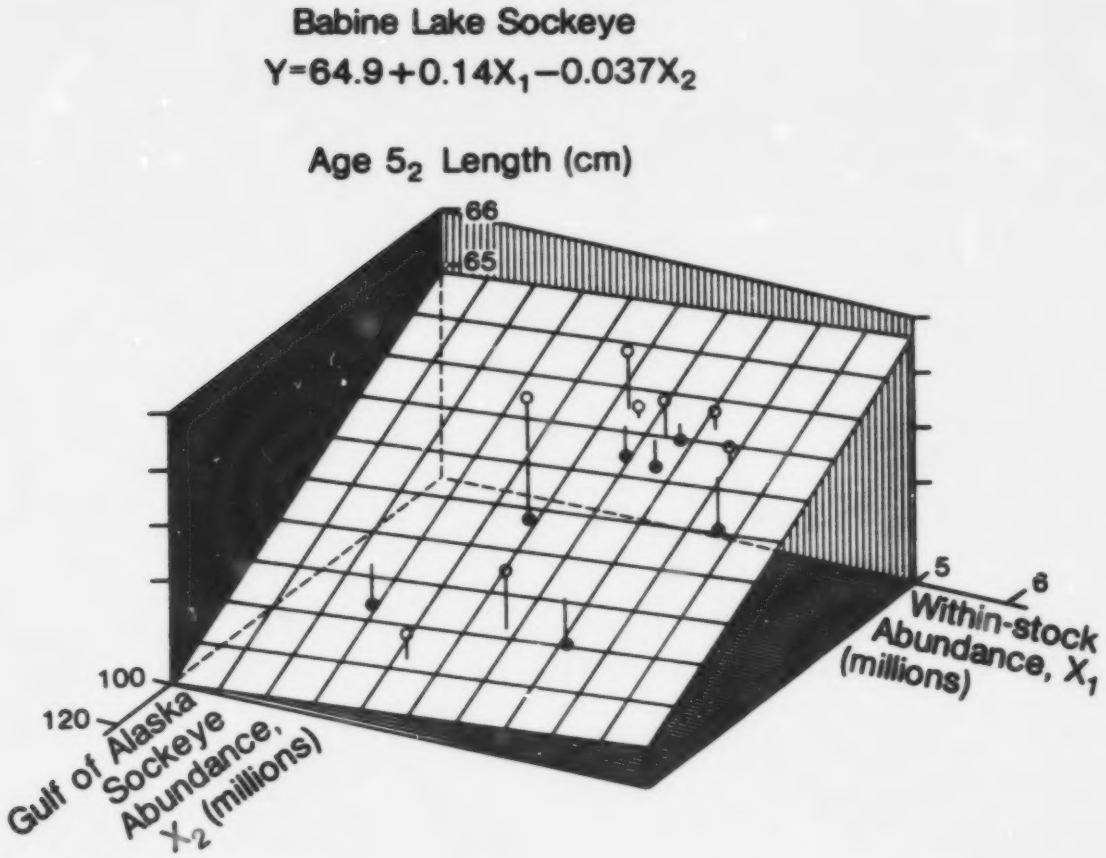

Fig. 5. Same as Fig. 4 except dependent variate is age 5_2 length of Babine Lake sockeye salmon.

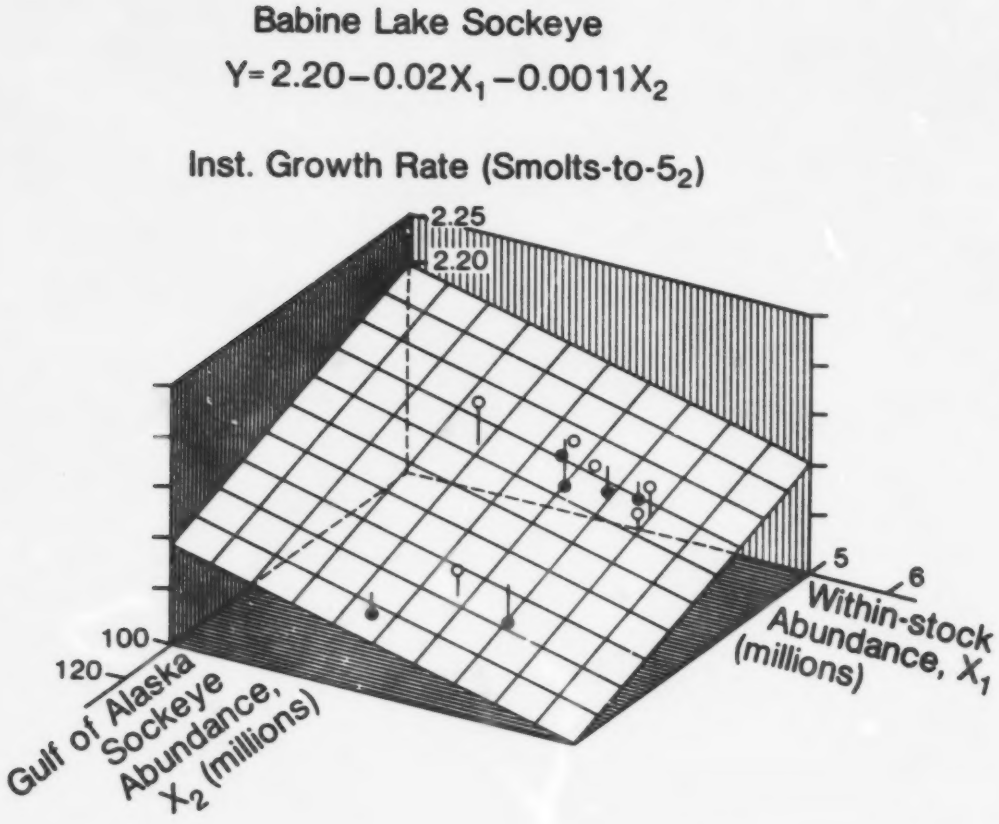

Fig. 6. Same as Fig. 5 except dependent variate is instantaneous growth rate from smolts to age 5_2.

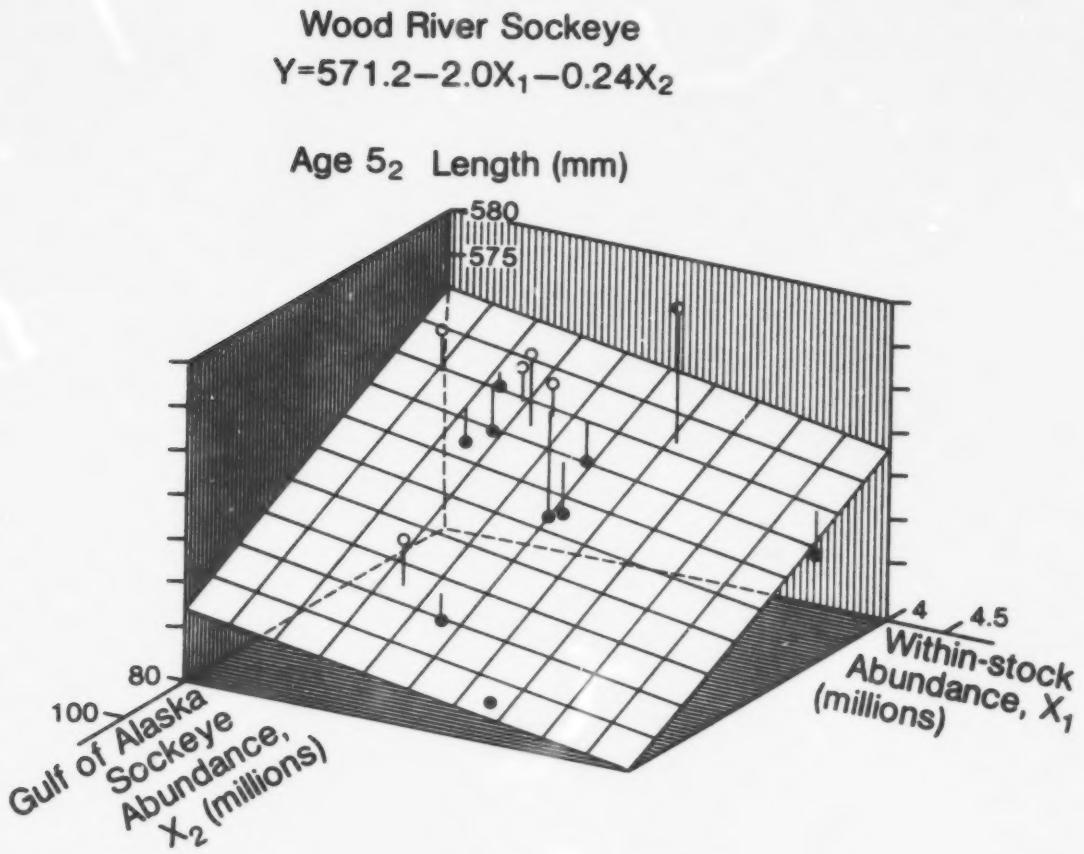

Fig. 7. Length of age 5_2 Wood R., Alaska, sockeye salmon as a function of ocean abundance of age 3 fish of that stock, X_1, and of age 3 fish of all stocks resident in the Gulf of Alaska, X_2.

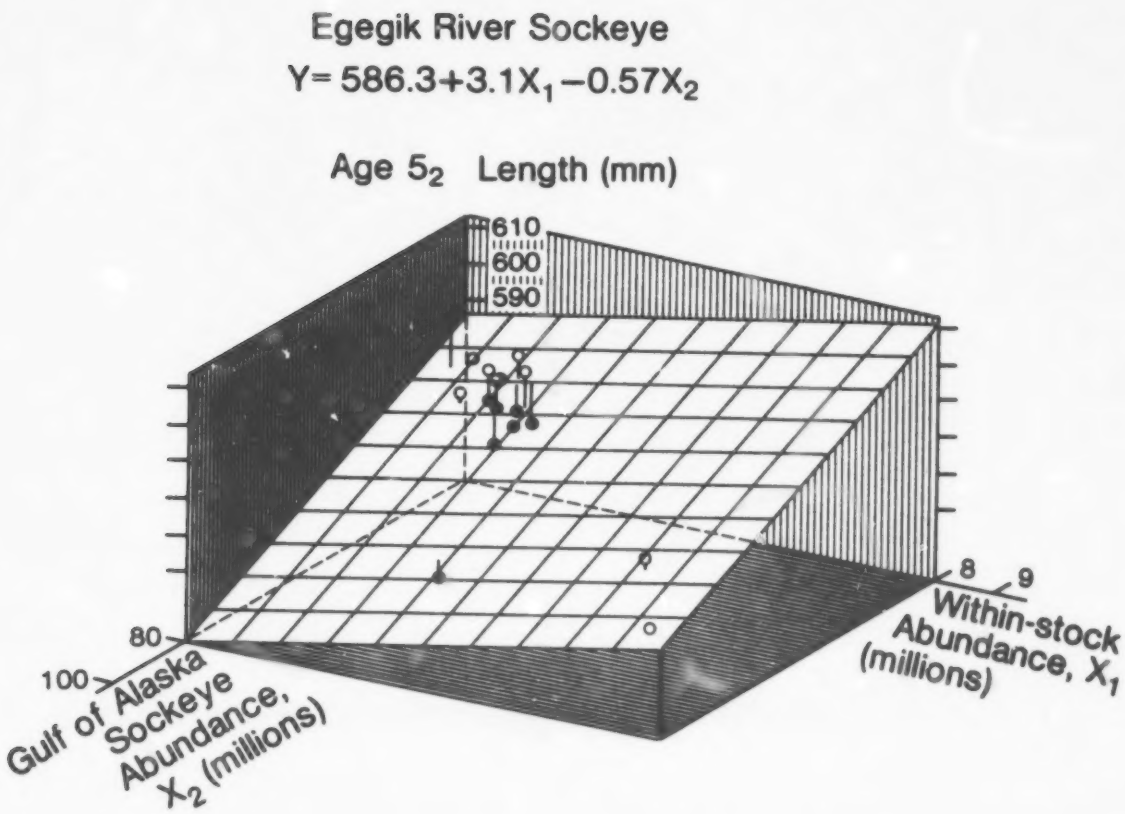

Fig. 8. Same as Fig. 7 except for Egegik R. sockeye salmon.

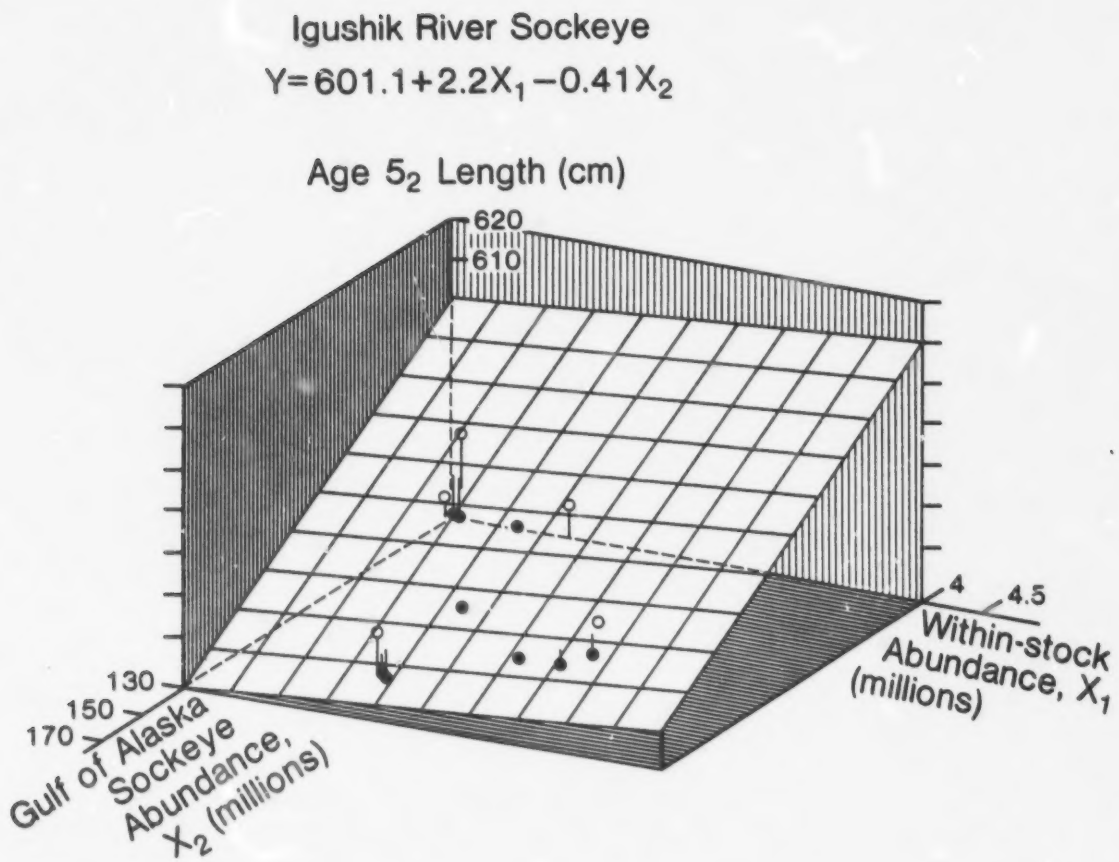

Fig. 9. Same as Fig. 7 except for Igushik R. sockeye salmon and ocean abundance of "all ages" used for X_1 and X_2.

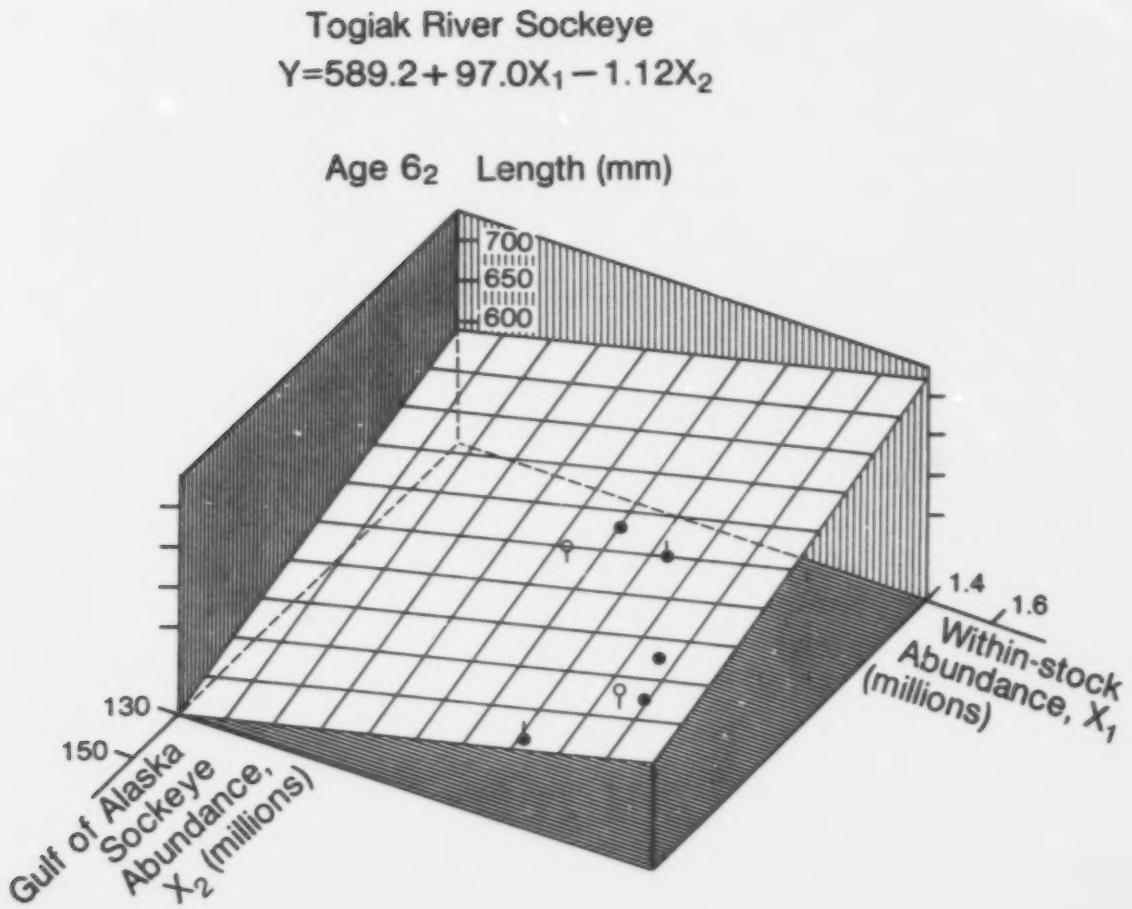

Fig. 10 Same as Fig. 9 except for age 6_2 lengths of Togiak R. sockeye salmon.

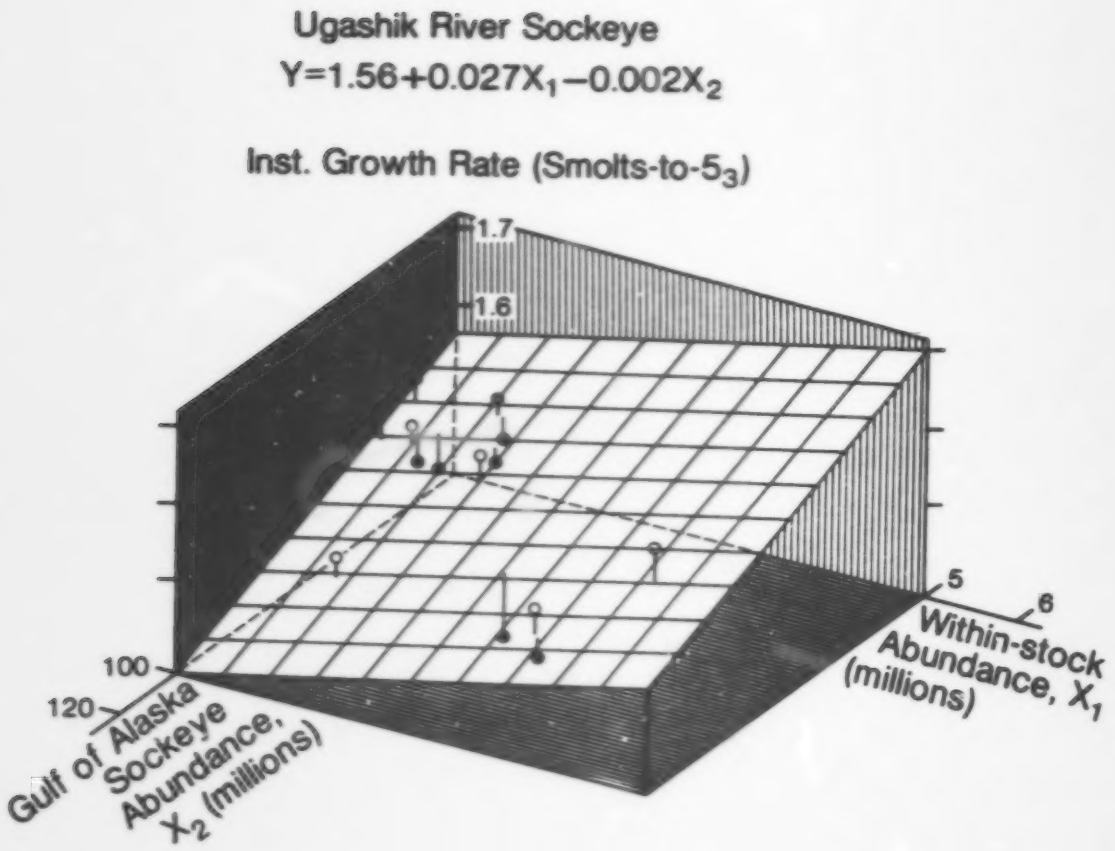

Fig. 11. Instantaneous growth rate from smolts to age 5_3 for Ugashik R. sockeye as a function of ocean abundance of ages 4 and 5 fish of that stock, X_1, and of ages 4+5 of all stocks resident in the Gulf of Alaska, X_2.

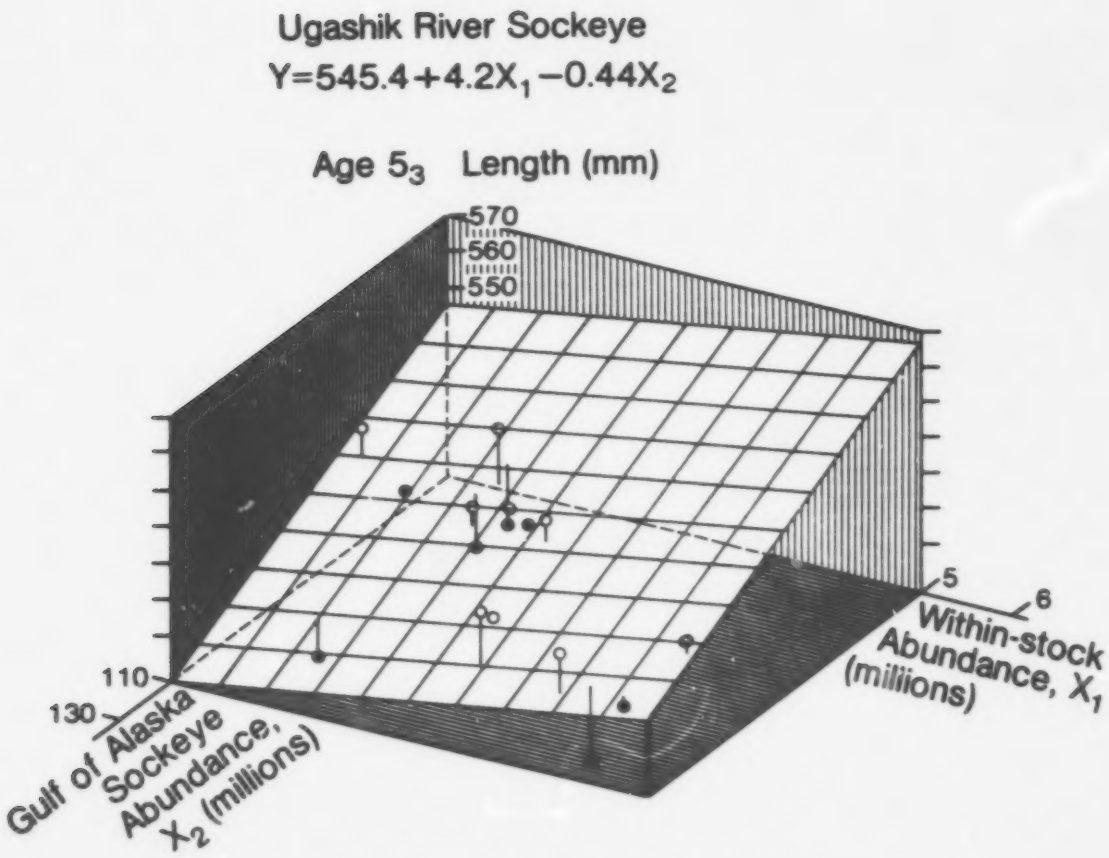

Fig. 12. Age 5_3 length of Ugashik R. sockeye as a function of ocean abundance of ages >2 of that stock, X_1 and of ages >2 of all stocks resident in the Gulf of Alaska, X_2.

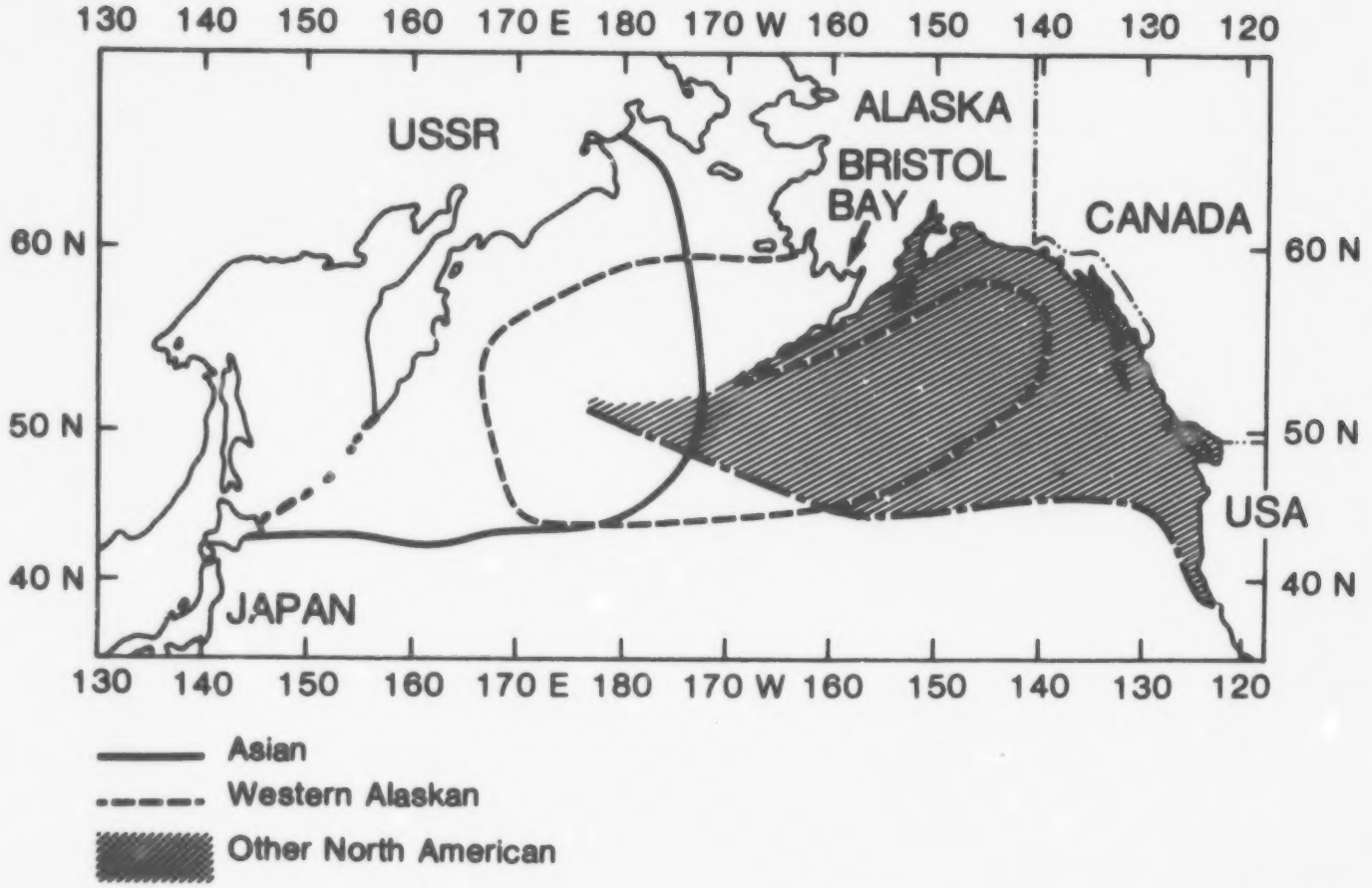

Fig. 13. General ocean distribution of sockeye salmon from Asian, western Alaskan (mainly Bristol Bay) and other North American stocks (mainly British Columbian), (adapted from French et al. 1976).

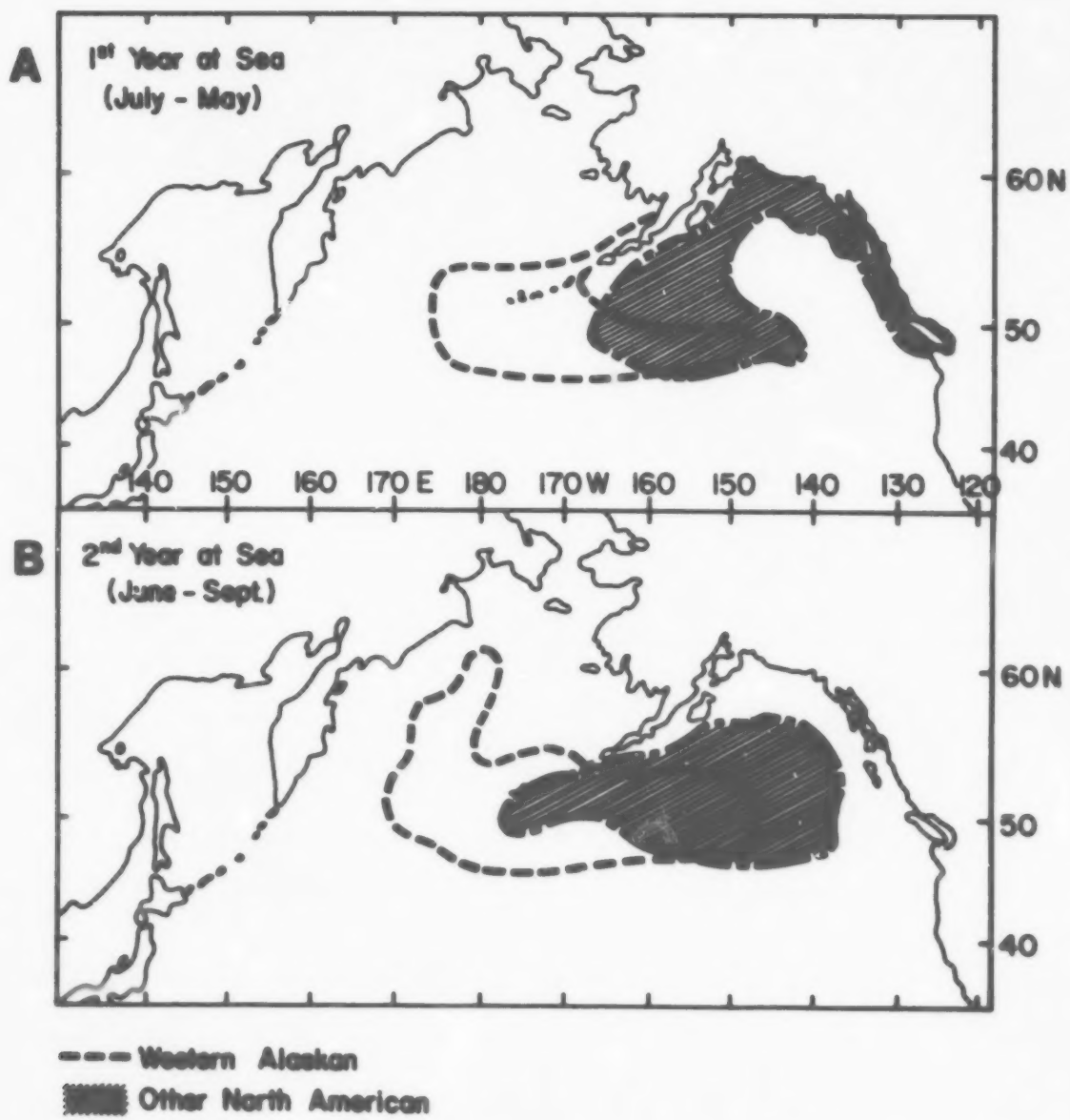

Fig. 14. Ocean distribution of sockeye salmon from western Alaska (open) and other North American stocks (hatched) during two segments of their ocean life (adapted from French et al. 1976, Figs. 93-94). Part A is for July-May of the first 12 months at sea, part B is for June-Sept. of the second year at sea.

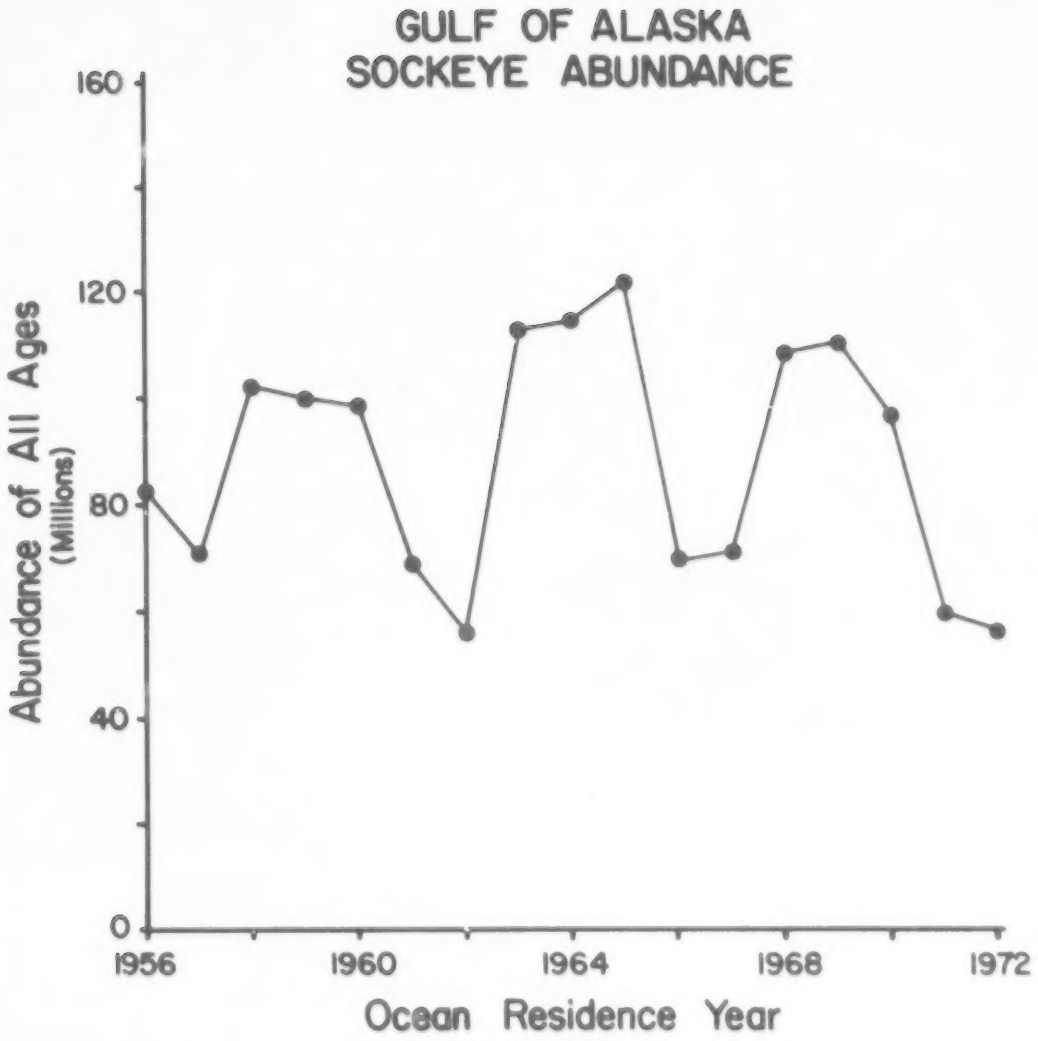

Fig. 15. Reconstructed minimum ocean abundances of sockeye salmon of all ages resident in the Gulf of Alaska (adapted from Peterman and Wong 1984).

Fig. 16. Same as Fig. 15 but from the sum of ages 2+3 only (adapted from Peterman and Wong 1984).